SYMPOSIUM ON PRIMARY PRODUCTIVITY AND MINERAL CYCLYING IN NATURAL ECOSYSTEMS

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Harold E. Young, Symposium Chairman
Carl D. Monk, 1967 Program Chairman, ESA

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SYMPOSIUM

PRIMARY PRODUCTIVITY AND MINERAL CYCLING IN NATURAL ECOSYSTEMS

ECOLOGICAL SOCIETY OF AMERICA

AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

13th Annual Meeting
New York City
December 27, 1967

Introductory Remarks

by

Harold E. Young

There is a growing awareness by mankind that the most critical problems facing the world are population growth, two percent per year, and rapid deterioration of man's environment. The solution of these problems and their corollaries challenge the efforts of scientists and non-scientists alike. To solve these problems, research must be conducted by scientists within a number of separate disciplines. The results must then be integrated into a series of action programs with little time before such programs must go into effect.

Ecologists are currently obtaining basic information on primary productivity and mineral cycling of natural ecosystems. This information will be the basis for producing more food and fiber to meet the requirements of the rapidly increasing world population and prevention of further damage to natural ecosystems as well as the rehabilitation of ecosystems that have deteriorated.

Internationally known scientists will present general principles and specific information today on primary productivity and mineral cycling in natural ecosystems. If these scientists, by their accomplishments, can encourage others to add to the pool of knowledge in this area, then a significant step forward will have been in the solution of the major world problems of over-population and environmental deterioration.

Recognition of nationwide problems may occur by basic scientists, applied scientists, professionals, or the general public. The impetus to solve such a problem may occur by one or more of these groups simultaneously. Solution will eventually involve all groups. To begin this symposium on an optimistic note, I would like to illustrate active relationship between these four groups in my own field, forestry.

Before doing so, I would like to point out that every university-trained forester receives instruction in silvics, a branch of ecology, and silviculture. Therefore, it should not be surprising that the Society of American Foresters, in a recently proposed statement on forest policy, included the following:

"The Society recognizes the interrelation of air, water, soils, plants and animals. It is keenly aware that ecology is basic to forest land management, and that man himself is a significant part of the ecological system."

The basic research by ecologists has done much to alert foresters to the importance of knowledge of primary productivity and mineral cycling in natural ecosystems. The full impact of their contributions became apparent during the recent fourteenth congress of the International Union of Forestry Research Organizations in Munich. Section 25, Growth, Yield and Forest Management, of IUFRO formed a working group to study the mensuration of the forest biomass. This group will be concerned with basic units of measurement and sampling procedures in preparation for the next congress. Suggestions and recommendations will be most welcome for the biomass concept is comparatively new to most foresters.

Applied research has been done in the eastern United States on the weight, nutrient element, and pulping characteristics of all of the components of complete mature trees and on some non-commercial woody perennials. These studies have shown that the logging residue contains one-third of the total fiber of the tree and that pulp can be made from every component except the branches of similar characteristics to pulp made from the bole. The woody perennials can produce about as much fiber per acre per year as trees and the stemwood of some species can be made into pulp of similar characteristics to some tree species. Recently the major forest products laboratories in both the U.S.A. and Canada have displayed interest in such applied research which they can perform on a large scale better than universities.

Professional foresters in their role as land managers are becoming increasingly concerned with application of a number of management techniques in order to meet the demand for forest products. This concern has, in turn, been communicated to the manufacturers of harvesting and milling equipment to permit greater utilization of more of each tree and shrub into more useful consumer products.

The public, affluent, urban, and mobile, seeks recreation in the forests in greater numbers each year. This compelling public desire to recreate in natural surroundings is forcing all forest managers to re-evaluate their forest policies and practices in terms of the multipurpose land use concept. Interest and pressure by the general public and by professional land managers has generated increased effort by scientists.

Everything that we eat is being produced at about ten times the yield of 100 years ago on fewer acres by fewer people. If this can be accomplished in the forests, then less land will be necessary to provide the primary forest products required for public consumption. This should result in large natural forests to be used primarily for watershed management and recreation.

Conservation, the wise use of our forests, depends on forest management that is ecologically sound and consonant with human needs. There is today, simultaneously, considerable interest and activity in all four aspects of our national problem of forest use. Progress is being made in the ecological health of our forests, hopefully at a rate equal to or greater than that of population expansion.

TREE BIOMASS ESTIMATION

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Introduction

As forestry and particularly forest utilisation become more intensive, there is a growing need to improve our understanding of the relationships between forest organisms, forest environments and the multiple uses of forest areas. These relationships influence the magnitude and pattern of the four major functional ecosystem processes, namely the flows of organic matter, energy, chemicals and water. Comprehensive studies of these, such as are envisaged for the International Biological Programme, necessarily involve biomass determination.

Because trees are so large, weight determinations of entire trees are laborious and the combined weight of all trees in a forest stand is normally determined from the weights of sample trees. Even in evenaged monoculture stands, trees vary in size and proportions so that care in the selection of sample trees is important. Usually the method of sampling is an arbitrary compromise between the available labour and resources and the accuracy required. In special experimental areas, such as fertiliser or tree species trials, sampling may be further restricted in the number and choice of trees available for weighing because of the need not to jeopardise the long term experimental aims.

Sampling introduces errors into the total weight determinations if the weight distribution of the sample trees does not exactly reflect the average stand dimensions. Misleading statements of the accuracy attained by particular methods may be made if the variability of the sample trees is incorrectly equated with the variability between trees in the stand.

The purpose of this paper is for one forest plot to compare the known tree total oven dry weight obtained by summation of the measured weights of all trees in the plot with the estimated weights that would have been obtained had various sampling methods been used. Comparisons are made for the trees as a whole (exclusive of roots less than 5mm diameter) and for the component parts - leaves, cones, branches, boles and roots greater than 5mm diameter.

Field and Laboratory Methods

A study plot 80 x 109 feet (0.081 ha) was marked out in the extensive plantations of Pinus radiata D. Don at Mt. Stromlo Forest near Canberra, Australia. The plot contained one hundred living trees, the location of each tree was mapped and its crown spread, height and bole diameter at breast height (4ft. 3in., 130cm) measured. In September 1966 each tree trunk was severed at ground level and the tree carefully lowered onto a tarpaulin to minimise loss of tree parts. Additional trunk and crown measurements were made on the felled tree (table 1).

Immediately after felling and measuring each tree, the oven dry weights of the component parts were determined as follows. All branches were cut from the bole and separated into living (i.e. with green leaves) and dead branches. The cones were picked from the branches and separated into male, current year female and previous year female and placed in paper bags for oven drying. The remaining crown (leaves and branches) was cut into suitable lengths and placed in large paper bags. The trunk was sectioned in five feet lengths (1.52m) and transported with the full paper bags to the laboratory two miles (3 kilometers) away for oven drying.

The paper bags and their contents were dried to a constant weight in a large forced air oven maintained at 85°C, crown material being stored in a cold room at 4°C until oven space was available. A preliminary trial showed temporary storage of plant samples in the cold room caused no appreciable change in dry weight. All crown drying was virtually complete within a week from tree felling after which leaves were separated from branches, and the dried cones, leaves and branches were weighed as complete groups for each tree. Whilst the crowns were oven drying, the bole sections were given a preliminary drying in a room heated to 60°C after which the entire bole sections were oven dried at 85°C and weighed.

Individual tree roots were extracted from the soil using a tractor winch and by hand digging. No attempt was made to collect fine roots but great care was taken to ensure all roots having a diameter greater than 5 mm were collected. After carefully brushing all soil off the roots they were cut into manageable pieces, oven dried at 85°C and weighed.

Since entire components of each tree were dried and weighed, the individual tree dry weights are believed to be reasonably accurate, although they would be slight underestimates because of unavoidable loss of some kinds of organic matter. Pollen and male cones were lost during the felling and breakdown of the trees but this loss would be less than 0.1% of the total tree weight. Some bark flaked from the trunk and branches but again this would be a small proportion of the total weight.

The Forest Stand

The study plot was on a flat site in an eight year old, unpruned, monoculture plantation of P. radiata and was typical of such plantations at Mt. Stromlo. One year old seedlings had been planted in 1958 at ten feet (3m) intervals along lines ripped seven feet (2m) apart to give an initial stocking density of 1500 per hectare. Due to natural causes, probably drought, this had decreased to about 1200 after eight years. The forest canopy had almost closed giving about 90% cover and the lowermost whorls of most trees and the ground vegetation were dead.

At clear felling for weight determinations, the average tree height was 26.2 feet (8 metres) and the average dry weight was just over 53 kilograms (tables 1 and 2). Despite the uniformity of management over the area, the trees varied considerably in size, the largest was about four times the smallest in crown and bole linear dimensions. The comparable oven dry weight range was even greater being 87x, 131x, 52x 54x and 49x for leaves, living branches, bole, root and total tree respectively. The frequency distributions of trees in general show a near normal slightly skew distribution for the various size parameters (fig. 1) measured.

The planting rows ran north to south and detailed comparisons of tree crown spread to the north, south, east and west of the boles revealed no consistent difference in development associated with orientation. Root examination suggested local soil conditions may determine tree size largely through their effects on root development. The soil varied locally from a medial red podzolic to a minimal yellow podzolic (Brewer, 1955). On the better aerated red soil with good permeability the trees had deep tap roots, sometimes several per tree, but elsewhere tap roots were poorly developed or absent, being replaced by a mass of finer roots. The large lateral roots ran in the top foot (30 cm) of soil.

Summation of the oven dry weights of all trees in the study plot gave a biomass of just over 66 thousand kilograms per hectare the relative percentages of cones, leaves, branches, boles and roots being approximately 1, 16, 27, 40 and 16 respectively (table 2).

Main Sampling Methods Compared

Three main types of sampling to determine the tree biomass of a plot were examined, namely

(a) Unit Area

All tree material in a prism extending above and below a sample area, or series of sample areas, is collected and weighed. The tree biomass for the plot is determined by converting the sample area data to a plot area basis.

(b) Average Tree

A tree, or number of trees, considered to be of average biomass are selected for weighing from a knowledge of the linear dimensions of the trees in the plot. The tree biomass for the plot is determined by multiplication of the weight of the sample tree (or average of the sample trees) by the number of trees in the plot.

(c) Regression Analysis

A number of trees, selected either randomly or systematically, are weighed and the mathematical relationship between the weights of the whole trees, or tree components, and one or more tree dimensions calculated. Knowing the relevant linear dimensions of all trees in the plot, the tree biomass for the plot is determined from the regression formulae.

Typical dimensions used in average tree and regression analysis methods for weight determinations are tree height, crown volume and the diameter and cross sectional area of the trunk at various heights (fig. 2, 3a and 3b). Since the cross sectional area of the bole at breast height gave relatively satisfactory relationships and can be easily measured all results are given on this basis unless otherwise specified.

Results

a. Unit area methods

Unit area sampling was not done in the study plot since this would have prevented the summation of individual tree weights to obtain an accurate reference value for tree biomass per hectare. Knowing the location, weights and crown plans of individual trees, the distribution of organic matter as dry weight over the plot could be simulated on the computer. By scanning the plot model, unit area methods could be applied to obtain estimates of tree biomass by various methods to compare with the known biomass value (table 3a). In practice, greater errors occur in using clip sampling methods than those given since crown weight in the model was considered to be uniformly distributed over the crown plan of individual trees. Because of the large size and complexity of forest ecosystems, further error might be introduced due to practical difficulties associated with accurate outdoor collection of material above and below the unit area.

Estimates of canopy weight per hectare proved to be more accurate than corresponding bole estimates largely because the crowns cover about 90% of the plot area whereas boles only occupy about 0.3%. For example, all 15 random squares of 3.34 sq.m. area contained some crown material whereas only eight included bole material. Generally, increasing the number and area of the sample units reduced the percentage error but even for the most intensive sampling used i.e. when almost 17% of the area was sampled, the average percentage error for total biomass for the ten random squares combined was 7%. When all possible unit areas over the study plot were considered using a model with a grid of 1 sq.ft. (0.09sq.m), for the four sample unit sizes, overestimates for bole and canopy were as high as 1869% and 329% respectively and underestimates 100% i.e. with no bole or canopy material present in a unit area (table 3b). The percentage errors for individual components such as cones, leaves and branches would probably be even greater.

Accurate clip sampling under outdoor conditions is very laborious and time consuming and unit area methods of determining plant biomass in forests appear to be inaccurate and inefficient when compared with other methods described later. The use of vertical enclosures in forests to determine community photosynthesis or transpiration on a stand area basis presumably would give equally erroneous results due to the problem of obtaining a suitable unit area. Increased efficiency might result if the sample squares could be located on the basis of biomass distribution rather than at random.

b. Average tree methods

Average tree methods assume it is possible to select a tree, or trees, which approximates to the average for all trees in total and component dry weights. The tree(s) may be selected by subjective sampling of trees of known dimensions or by objective sampling from the whole population e.g. by systematic sampling.

As an example of systematic sampling, all possible combinations of the weights of either every fifth, tenth or twentieth tree in the plot were grouped and averaged for each combination. The averages were multiplied by the number of trees in the stand to give the total biomass (table 4a). The results, expressed as percentage errors of the known stand weights, decreased with increasing numbers of weighed trees but even with a 20% sample large errors (over 10%) occurred.

To improve the previous procedure, the average ratio of dry weight to bole cross sectional area at breast height was calculated for every combination group and multiplied by the total bole cross sectional area of the stand. This adjustment compensated for samples having exceptionally large or small cross sectional areas relative to the stand average and resulted in a marked improvement in the accuracy of estimated stand weights (table 4b).

A different average tree approach is to try to select a tree or trees having dry weight distribution values corresponding to the stand average. No single tree in the study plot exactly met this requirement for all tree components. In order to select the trees most approaching this ideal, cross sectional bole area at breast height was used as the basis for selection.

The component weights of the tree of nearest average bole cross sectional area, and the average weights of groups of trees having bole cross sectional areas closest to this tree, were multiplied by the total number of trees per hectare to determine biomass and the percentage errors against the known biomass (table 4c). Repeating the procedure for trees with smaller or larger boles than the average gave no improvement in accuracy. For corresponding numbers of sample trees, sampling around the average tree generally gave better results than systematic sampling. However, estimates of the weight of components such as male cones, female cones and dead branches based on average trees were much more inaccurate, the weights of these components not being related to bole cross sectional area. In fact none of the five trees closest to the average carried any female cones. Since cones and dead branches represent only a very small proportion of tree weight, the percentage error for the stand biomass is nevertheless reasonably accurate. Where accurate cone and dead branch weights are required, it would seem better to estimate these components separately using some systematic sampling of only those trees carrying cones or dead branches respectively.

In some situations average tree sampling might have to be restricted to one or two trees. Bole cross sectional area, tree height, crown diameter and crown depth were considered together and given equal ranking to test if this improved tree selection for weight estimates with a limited number of sample trees. Combining these characters in this way gave a remarkable improvement in biomass estimates for one tree sampling although errors in cone and dead branch estimates remained considerable.

c. Regression analysis methods

Regression analysis methods assume for the population a relationship between tree or tree component weights and some other easily measured parameter or combination of parameters. Whilst major tree components are related linearly to the parameter adopted in this study, namely bole cross sectional area at breast height, no significant relationship existed for minor components such as cones and dead branches (fig. 3a and 3b). Consequently, relatively large errors were obtained for estimates of the weight of the minor components but these, because of their small proportionate representation, had little effect on total biomass estimates. It should be emphasised regression equations of high significance could be derived by chance for particular sets of sample trees which if used to estimate the weights of the whole population would give very incorrect estimates of stand weight (figs. 2 and 3).

Under certain circumstances, biomass determination by destructive tree sampling may be restricted to certain trees within a stand e.g. the largest trees, the smallest trees, the average trees or some combination of average, large and small trees. When sampling is restricted to trees from a very small group of the population, regression analysis methods are not particularly appropriate and may give large errors (table 5a).

Sampling based on the five largest trees, which contain 10% of the stand weight, gave more accurate estimates than those based on the smallest trees,0.5% of the stand weight, because the largest trees extend over a greater size range and are more representative of the stand biomass. For this study plot and the various kinds of restricted tree selection examined, regression analysis gave the most accurate results when based on the group of trees around the average, extending the sample spread about the average by including more than the five trees gave little improvement in accuracy.

In order to obtain a better distribution of sample trees over the population for regression analysis, the whole population was divided into five or ten equal tree number or size classes and the sample trees were selected as being the nearest to the averages of each class (table 5b). Apart from cones and dead branches the biomass estimates were reasonably accurate, tree classification by numbers being superior to that by size and no great improvement in accuracy was obtained by increasing the number of sample trees from 5 to 10.

Where trees are selected randomly from the population for regression analysis the potential error is considerable even though the probability of obtaining the greatest possible percentage error is small. Percentage errors for the most accurate and least accurate results for ten random regression lines each based on five trees are given for random sampling in the whole population and for stratified random sampling according to number or size classes of trees. Of these two kinds of regression analysis methods stratified sampling seems the more reliable.

Conclusions

A more detailed statistical treatment of the data is under way but this preliminary study in which some sampling methods used in biomass investigations are applied to a known population of trees draws attention to sampling problems and the magnitude of errors likely to occur in biomass estimates for a conifer plantation. In this way it may provide guidelines on methods to obtain biomass data at minimum cost. The stand was fairly typical and the results probably have implications of wider application to biomass sampling for forests of this nature. Average tree and regression analysis methods were more satisfactory than unit area methods, particularly for the major tree components, largely because bole cross sectional area at breast height and tree weight were related linearly. The best of the average tree and of the regression analysis methods gave comparable accuracies for the same intensity of sampling. These methods could also be applied in more diverse forests with a multiplicity of tree ages and species, provided the population was grouped appropriately for sampling.

Reference

Brewer, R. 1955. The Australian Capital Territory as a region. 44-47. Ed. H. L. Whyte. Halstead Press, Sydney.

Acknowledgements

The authors are grateful to the Australian Research Grants Committee for financial assistance.

TABLE 1. Range of tree size (cm) in study plot of 100 trees

	Maximum	Minimum	Average
Tree height	1018	268	800
Crown depth to lowest living branch	994	256	760
Crown diameter	549	107	335
No. of living branches	154	29	78
No. of whorls with living branches	26	5	13
Bole diameter at ground level	20.9	5.8	16.8
Bole diameter just below lowest living branch	21.5	5.1	15.9
Bole diameter at breast height (130 cm)	21.6	3.9	13.0

TABLE 2. Oven dry weights

	Single trees (kilograms)			All trees (kilograms per hectare)
	Maximum	Minimum	Average	
Male Cones	1.42	0	0.22	277
Mature female cones	2.84	0	0.12	148
Immature female cones	0.06	0	0.01	10
Leaves	28.80	0.39	8.46	10,457
Living branches	50.66	0.39	13.63	16,840
Dead branches	3.31	0	0.84	1,040
Bole	43.94	0.85	21.62	26,709
Roots with diameter greater than 5mm	24.13	0.45	8.56	10,573
Total (exclusive of fine roots)	149.57	3.07	53.47	66,054

TABLE 3a. Percentage errors in stand oven dry weight estimates using unit area methods

Five random square plots

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
% of area sampled	0.5		2.1		4.7		8.3	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Canopy	-4	-46	-12	-36	-2	-29	-11	27
Bole	-100	1402	-60	-100	-1	-100	9	-100
Total	-25	673	-35	-66	1	-61	1	-54

Ten random square plots

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
% of area sampled	1.0		4.2		9.4		16.6	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Canopy	8	100	7	60	-1	-32	2	92
Bole	-100	1205	-39	146	24	-100	9	105
Total	-11	584	12	72	-4	-65	8	94

TABLE 3b. Percentage errors in stand oven dry weight estimates using unit area methods

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
Maximum possible number of samples based on a square grid of 0.1 sq.m.	8346		7800		7272		6762	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Canopy	329	-100	282	-100	262	-94	195	-81
Bole	1869	-100	392	-100	241	-100	204	-100

TABLE 4a. Percentage errors in stand oven dry weight estimates using average tree (s) methods

Systematic sampling

Method	Every twentieth tree			Every tenth tree			Every fifth tree		
Number of trees averaged per group	5			10			20		
Possible number of combinations	20			10			5		
Grade	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average
Male cones	-0.1	101	32	-4	33	19	-4	33	15
Female cones	3.4	388	90	-5	161	70	31	-82	62
Leaves	-1	51	21	-1	33	14	5	-18	11
Living branches	2	-40	22	1	37	17	4	22	14
Dead branches	-1	-72	26	1	52	25	6	29	20
Boles	-1	-47	21	-4	-28	16	3	-20	12
Roots	1	59	26	-3	-34	21	-1	-34	14
Total trees	0.4	-44	21	-4	32	17	3	-20	12

Average percentage errors estimated by disregarding algebraic signs.

TABLE 4b. Percentage errors in stand oven dry weight estimates using average tree(s) methods

Systematic sampling with proportionate adjustment to stand bole cross sectional area

Method	Every twentieth tree			Every tenth tree			Every fifth tree		
Number of trees averaged per group	5			10			20		
Possible number of combinations	20			10			5		
Grade	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average
Male cones	1	72	27	-1	28	11	-1	14	6
Female cones	6	395	88	-10	148	68	23	-82	58
Leaves	0.3	16	6	0.5	10	4	0.3	5	2
Living branches	0.4	-24	6	-0.3	-14	6	2	-8	5
Dead branches	-0.1	71	31	8	45	28	-8	-32	16
Boles	0.2	-13	5	0.1	-9	4	0.1	-5	3
Roots	2	-29	9	3	-17	7	-1	-8	5
Total trees	1	10	5	0.2	-9	4	2	-5	3

Average percentage errors estimated by disregarding algebraic signs.

TABLE 4c. Percentage errors in stand oven dry weight estimates using average tree methods

Sampling around the tree of average bole cross sectional area

Method Number of trees averaged	Trees closest to average bole cross sectional area					Trees closest to average for bole cross sectional area, height, crown diameter and depth graded equally	
	1	2	5	10	20	1	2
Male cones	-94	-63	-23	8	-6	-30	18
Female cones	-100	-100	-100	-78	-62	-99	-100
Leaves	9	11	7	2	-0.1	9	10
Living branches	-22	-5	0.5	-3	-7	11	-4
Dead branches	-44	19	-37	-23	-14	-60	-69
Boles	17	12	2	5	4	-3	-3
Roots	10	6	-1	-2	-3	-2	-10
Total trees	3	6	1	1	1	1	-3

TABLE 5a. Percentage errors in stand oven dry weight estimates using regression analysis methods

Restricted choice of trees based on bole cross sectional area

Method	Smallest trees	Largest trees	The smallest and the largest tree, and three trees closest to average	Trees closest to average		
Number of trees used	5	5	5	5	10	20
Male cones	-101	168	35	-18	8	-10
Female cones	-100	-76	95	-100	-76	-68
Leaves	-21	-2	12	8	3	2
Living branches	-70	13	22	-3	-6	-4
Dead branches	-151	69	-20	-41	-22	3
Boles	-22	28	-10	3	5	5
Roots	-77	-17	4	-2	-3	-3
Total trees	-45	13	3	0.2	0	0.7

TABLE 5b. Percentage errors in stand oven dry weight estimates using regression analysis methods

Subjective tree selection within strata over the whole population range

Method	Average tree in each of 5 equal number classes	Average tree in each of 10 equal number classes	Average tree in each of 5 equal size classes	Average tree in each of 10 equal size classes
Number of trees used	5	10	5	10
Male cones	25	51	6	57
Female cones	-21	-60	-91	172
Leaves	-5	-3	16	10
Living branches	5	7	20	23
Dead branches	-20	11	-42	-17
Boles	-2	-3	1	-6
Roots	-5	4	-6	2
Total trees	-1	1	6	6

TABLE 5c. Percentage errors in stand oven dry weight estimates using regression analysis methods

Random selection of trees

Method	Random trees in whole population		Random tree in each of 5 equal number classes covering whole population		Random tree in each of 5 equal size classes covering whole population	
Number of random regressions	10		10		10	
Number of trees per regression	5		5		5	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Male cones	-1	102	-16	88	-2	102
Female cones	-16	627	-7	375	-36	-100
Leaves	-1	29	4	15	-0.3	20
Living branches	-1	-18	1	9	1	21
Dead branches	3	-77	-1	89	-3	59
Boles	3	-10	-1	8	1	-11
Roots	1	25	2	21	1	-17
Total trees	0.1	10	1	7	0.1	3

FIG 1. TREE SIZE FREQUENCIES

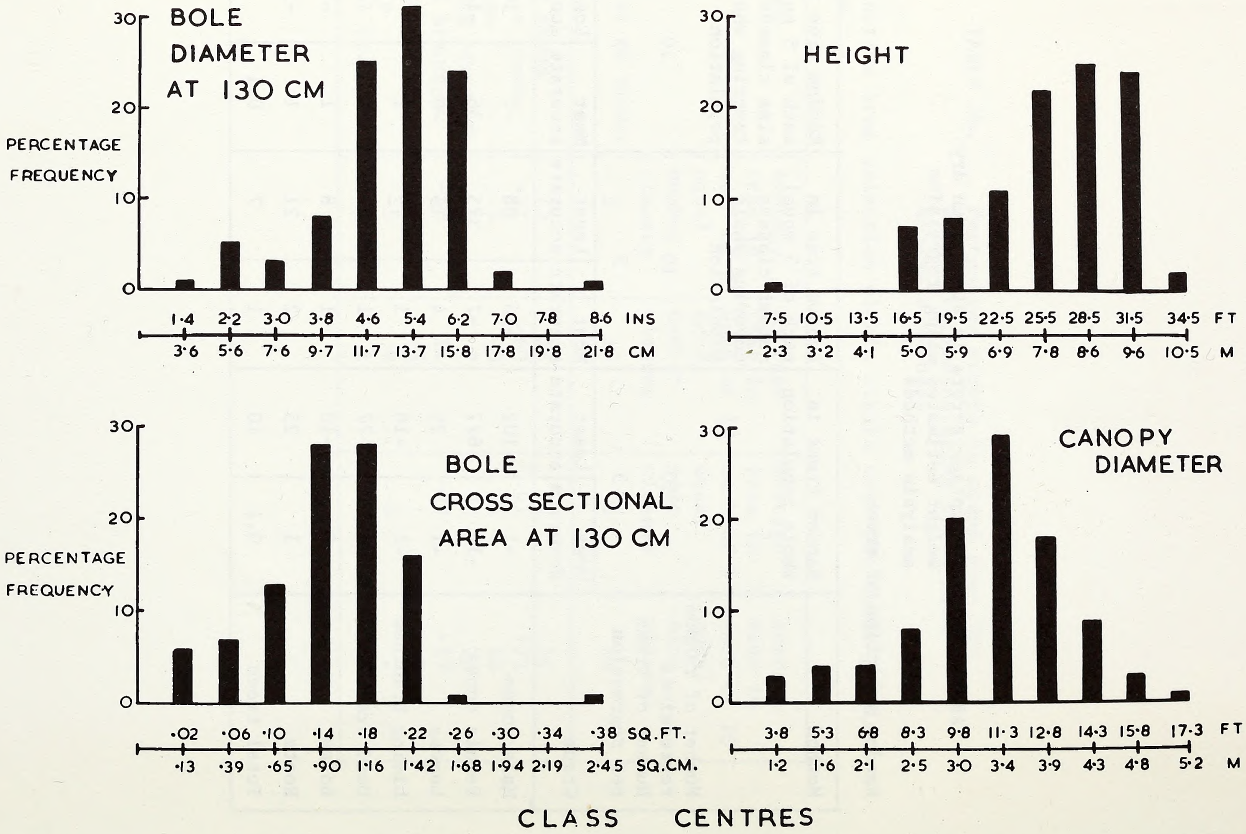
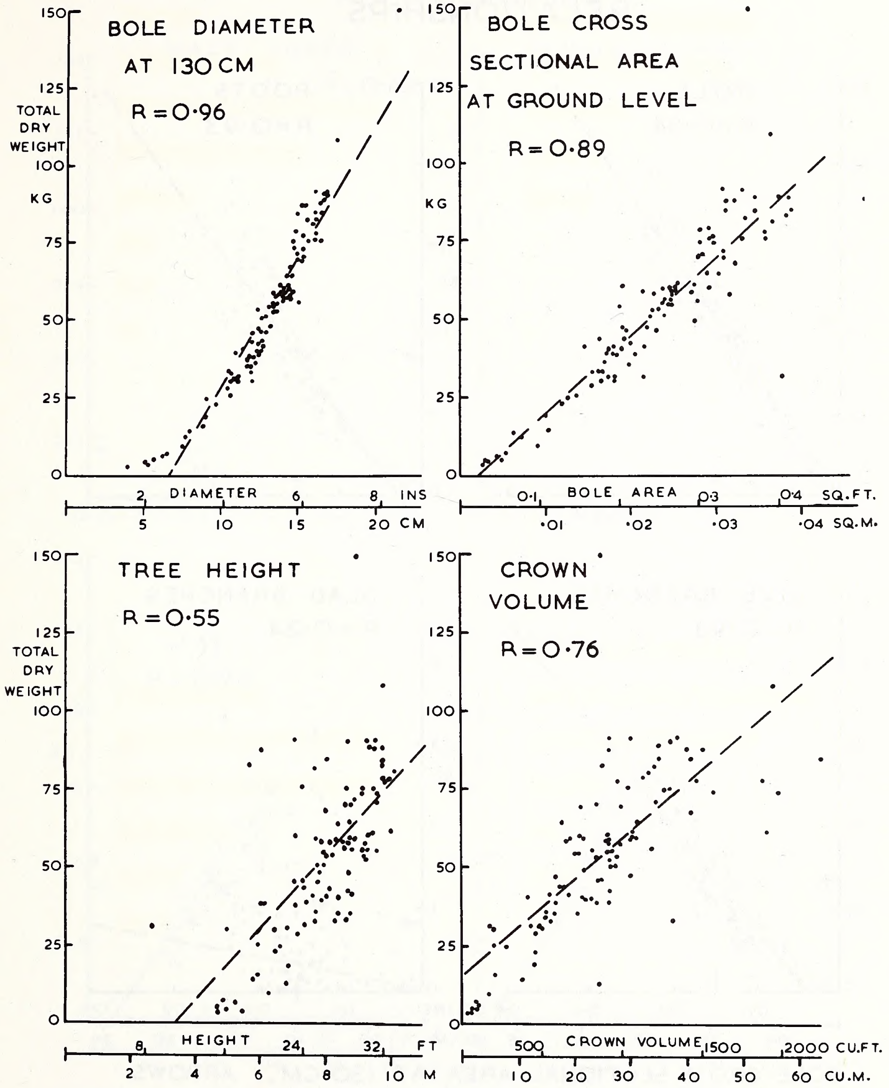


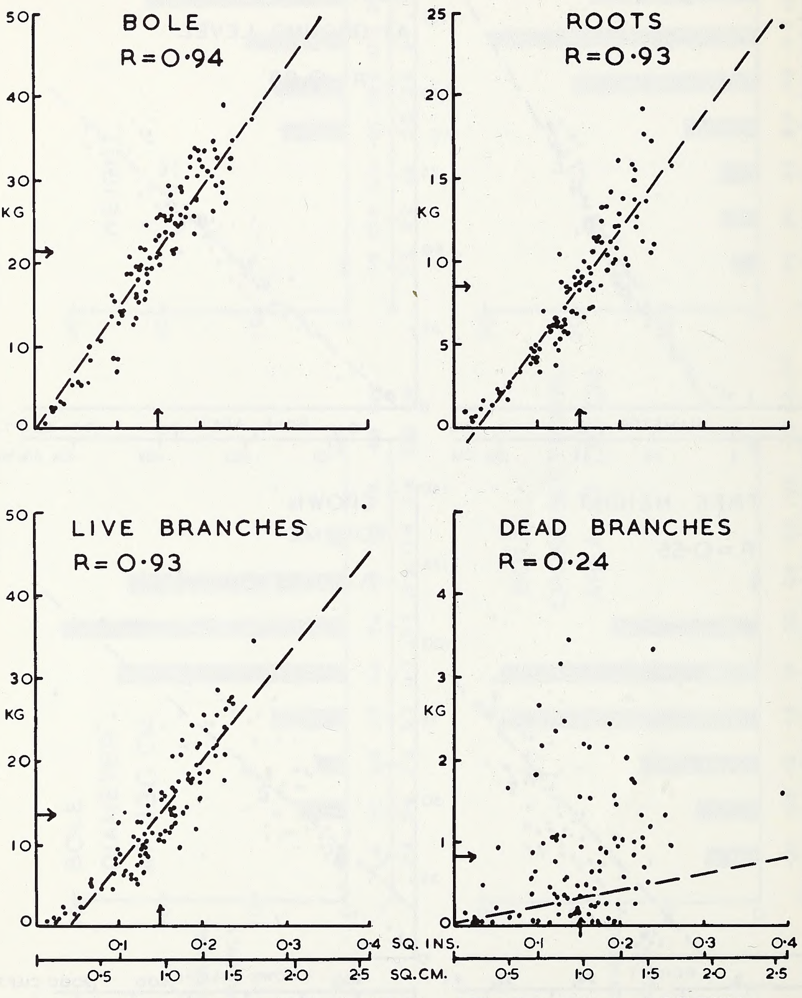
FIG. 2.-TOTAL DRY WEIGHT — TREE SIZE RELATIONSHIPS



R = CORRELATION COEFFICIENT

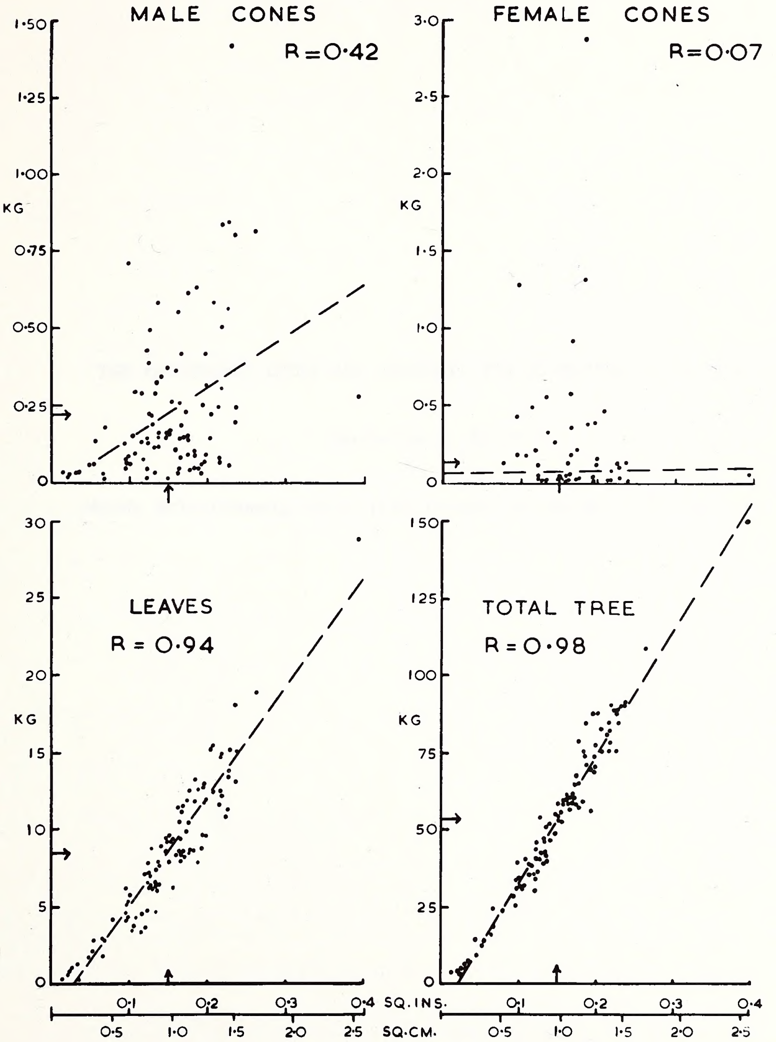
FIG. 3A

DRY WEIGHT — BOLE CROSS SECTIONAL AREA RELATIONSHIPS



BOLE CROSS SECTIONAL AREA AT 130 CM. ARROWS INDICATE AVERAGES. R=CORRELATION COEFFICIENT.

FIG. 3B
DRY WEIGHT — BOLE CROSS SECTIONAL AREA RELATIONSHIPS



BOLE CROSS SECTIONAL AREA AT 130 CM. ARROWS INDICATE AVERAGES. R = CORRELATION COEFFICIENT.

THE PHOSPHORUS CYCLE AND PRODUCTIVITY OF MARINE PHYTOPLANKTON

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The Phosphorus Cycle and Productivity of Marine Phytoplankton

by

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The rate of production of organic material in the oceans is dependent upon the availability of the essential plant nutrients and the rate at which these nutrients can be supplied to the phytoplankton organisms. To this extent the production of organic matter in the sea is similar to production on land, but almost all other aspects of the problem, including many of the techniques used to evaluate productivity, offer dramatic contrast to the terrestrial environment.

One of the most frustrating differences is the mobility of the marine populations. In the terrestrial environment one can blaze a tree and come back year after year and measure its growth, or one can establish quadrats which can be revisited time after time and the population density and the changes evaluated. This type of approach is not possible in the marine environment because the constant motion of the water continuously brings different populations to a given geographic location. Over large parts of the ocean horizontal differences in population are slight so that these can and frequently have been ignored. The water mass may be tagged with a drifting buoy so that repeated observations can be made on the same population from time to time. This technique, however, is suitable only for relatively short periods, and

(Contribution No. 2146 from the Woods Hole Oceanographic Institution.)

then only when the water does not move into an area of greatly different depth.

The productivity of the sea varies dramatically from place to place and the range of values is quite similar to the range that one finds in comparing deserts, grasslands, and forests. There is, however, a marked contrast between the size of the standing crop in the marine and terrestrial environments. It has been estimated by Ryther (1960) that the plant biomass in the oceans is only 0.1% of the total plant biomass on earth, but that this small population contributes 40% of the annual world production of organic matter. The large production which results from such a small standing crop in the marine environment is an indication of the rapidity of the turnover of the population. Practically all of the photosynthesis of the sea is carried on by microscopic plants which can, under ideal conditions, double their population size daily. In contrast to this it takes 50 years or more to develop a forest (90.5% of the biomass) and the rate of annual production (25% of the total) is a small fraction of the standing crop at any one time.

In a climax forest community the net annual production may be negligibly small because the death and decay of the older members of the stand balances the production of new plant material. This contrasts with crop lands where the annual production is harvested by man, or with pasture lands where the daily production is grazed by animals which produce meat or milk which is harvested. The marine environment falls midway between these two extremes. The phytoplankton crop is heavily grazed by zooplankton which, in turn, feed the fishes, but only a very small proportion of these are harvested. On an annual cycle, therefore, the net production of organic matter in the sea is small, just as it is in a climax forest. During the year, however, many generations of plant species may succeed one another, but the organic matter is consumed nearly as fast as it is produced.

On the basis of the above facts, it is clear that one cannot harvest the phytoplankton crop, weigh it, and determine the production of organic material during the course of a year. This would be a gross underestimate of the total amount of phytosynthetic production of organic matter. This forces the marine ecologist to use indirect methods for estimating the productivity of the oceans.

Some of these indirect methods depend upon the changes in the amount of chemicals involved in the production process, such as nutrients, oxygen or carbon dioxide. When changes in these characteristics of the environment are measured for a short period of time a valid evaluation of the rate of photosynthesis can be obtained. Experimental methods can also be used for determining the rate of photosynthesis on an isolated sample of the natural population. Observation of the changes in the oxygen content of the water or of the rate of assimilation of carbon dioxide as measured by C^{14} fixation are commonly used experimental methods. These give an instantaneous or short term evaluation of the rate of the process and must be repeated frequently to get an annual mean.

When one considers the immensity of the oceans, and the scarcity of biological oceanographers, it is not surprising that our estimates of the total annual productivity of the oceans are uncertain and incomplete.

The major reservoirs of the nutrient elements and the processes which transfer elements from one reservoir to another are shown diagrammatically in Figure 1. It will be immediately obvious to all that the best known of the marine living resources, the fishes, have been omitted. While their participation in the cycle is important, the nutrient content of the fish reservoir probably rarely exceeds 1% of the total and our analytical methods are not accurate enough to evaluate their contribution to the recycling problem.

The intensity of sunlight, the energy source which drives the system, decreases logarithmically with depth in the water column. Adequate sunlight for the net production of organic matter penetrates only to a depth of 100 meters or so even in the clearest ocean water. The surface waters are also warmed by the incident radiation and are generally isolated from the deeper waters by a density gradient, or thermocline, which decreases the rate of mixing between the large reservoir of nutrients in the deep water and the populations in the surface water which require these nutrients for their growth.

The process of photosynthesis is shown by the black arrow in Figure 1 because this is the one process that we can measure accurately and well using experimental methods on isolated samples of the population. We also know enough about grazing by the zooplankton on the phytoplankton population to permit estimation of its effect when the size of the two populations is known. The open arrows show processes concerning which we have little or no quantitative information. These include the direct excretion of nutrients into the water by both phytoplankton and zooplankton, the death of these organisms with the consequent release and decomposition of dissolved organic materials. These are major pathways for the recycling of nutrients and, over large parts of the ocean, the rate of organic production must depend heavily upon the rates at which these transformations occur.

Because adequate light for photosynthesis is limited to the near-surface waters, and because these waters are isolated by density stratification from the deeper waters, the growth of phytoplankton rapidly depletes the nutrients in the euphotic zone. An example of this effect is shown in Figure 2 which compares the phosphorus content of the water column at the beginning and the end of a ten-day "springbloom" period in the Gulf of Maine (Ketchum and Corwin, 1965). Here the euphotic zone was only 50 meters deep. During this brief period, nearly 50% of the available phosphorus was removed from solution and this amount was found in the particulate material, including the living population, and in dissolved organic phosphorus compounds. The total production of organic material during this ten-day period was only about 2% of the annual rate of production (Redfield et al, 1937, Ketchum, 1947) but nearly half of the available nutrient supply in the euphotic zone was consumed. It is obvious, therefore, that recycling and vertical mixing are essential in order to maintain the productivity of the phytoplankton population throughout most of the year.

The areas of high production of the world oceans are shown by the shaded areas in Figure 3. This chart was derived by Sverdrup (1955) and is based entirely upon a knowledge of physical oceanography, specifically, the expected amount of mixing and upwelling, specialized mechanisms which deliver the essential nutrients to the surface layers. Off the west coast of continents, for example, such as Africa and South America, persistent trade winds move the near-surface waters offshore and permit upwelling of waters with high nutrient concentrations from intermediate depths. In southern oceans, off Antarctica, there is a major current flowing completely around the earth, and associated with this current is a divergence which again brings nutrient rich waters close to the surface. The currents in the equatorial regions are also associated with divergence of surface waters. The great fishing banks, such as Georges Bank and the Grand Banks in the North Atlantic, are comparatively shallow areas where wind stirring and tidal mixing enrich the surface waters and increase the productivity. The effect of river drainage carrying nutrients into the sea is important in coastal waters and in semi-confined bodies of waters such as the Gulf of Mexico. However, in terms of the total oceanic production, river drainage adds only about 1% of the total nutrient requirement each year (Emery et al. 1955). Thus while river drainage is locally important, its value to productivity of the sea has been greatly over-emphasized by some.

There are vast areas of the ocean where the productivity is low. For these large areas no active mechanism is present to enrich the surface waters and the primary production must depend upon two processes, the regeneration of nutrients in the biological cycle and the vertical mixing and transport of nutrients from deeper waters to the surface. Unfortunately little is known about these two processes and they are not amenable to evaluation by laboratory experimentation.

Recent improvements in technique have made it possible to evaluate the relative importance of these two processes in nature. We have recently studied the phosphorus cycle in the Gulf of Maine in March, before the spring bloom, in April during the bloom and in September when the system is in a quasi steady state with little or no net change in the size of the population. The total amount of phosphorus under a unit sea surface area to the bottom at about 200 meters showed little difference at these three times, so that the entire cycle could be measured within the water column without considering losses to or additions from the bottom.

The distribution of phosphorus in the particulate material, in the organic compounds dissolved in the water and in the inorganic phosphate fractions is given for four depth intervals in Figure 4. The increase in particulate phosphorus during the spring bloom is clearly shown in the euphotic zone, the upper 50 meters of the water column. Some of this material sank to the layer immediately below but very little change was found in the amounts of particulate phosphorus at depths greater than 100 meters. Below the euphotic zone most of the total phosphorus was always present as available inorganic phosphate dissolved in sea water. Only in the near-surface waters at the height of the bloom did the particulate phosphorus approach 50% of the total amount in the water.

The changes in the distribution of phosphorus in these three fractions permit an evaluation of the importance of the various mechanisms which are involved in maintaining phytoplankton production at different times of year. The various sources of supply of phosphorus to the cycle of production are given in Table 1. In the pre-bloom period 28% of the required phosphorus was removed from solution in the water column and 72% was provided by vertical mixing. At this time of year no measurable amount of the required phosphorus was supplied by regeneration. During the bloom period, 86% of the required phosphorus was obtained by removal of inorganic phosphate from solution, 12% was provided by vertical mixing and 2% by regeneration. When the system was in a quasi steady state condition 43% of the required phosphorus was provided by regeneration and 57% by vertical mixing. This was not a true steady state condition since the amount of inorganic phosphate increased in the euphotic zone during the period of observations and this amount must also have been supplied by vertical mixing.

The fate of the phosphorus fixed in the organic cycle under these three sets of environmental conditions is shown in Table 2. During the pre-bloom period 13% of the phosphorus assimilated was found in the particulate matter about evenly divided between the euphotic zone and greater depths, but most of the phosphorus assimilated appeared as dissolved organic phosphorus in the deeper water. During the bloom, 92% of the phosphorus assimilated was found in the particulate matter, about half of which remained in the euphotic zone and the balance was found at greater depths. During the steady-state condition only 3% of the amount of phosphorus assimilated was found in the particulate fraction, which included an actual loss from the surface layers and a gain in the deeper water. At this time, 54% of the phosphorus assimilated was found in the dissolved organic form and the remaining 43% was regenerated as inorganic phosphate in the surface layers. These results emphasize again the importance of the rapid turnover of phytoplankton populations since, under steady-state conditions, only a small fraction of the material assimilated in the production process can be found in the living part of the population and a very large percentage of the phosphorus required by the cycle is regenerated to be used again.

The requirement for nutrients by the observed production of organic matter is compared with the available supply in the water column and with the amount already fixed in the standing crop by the data in Table 3. The conditions at both the beginning and end of each period of observations are used in this comparison. During the pre-bloom period, the production process required about 2.5% of the available supply of inorganic phosphorus in the euphotic zone and the available supply in the water would consequently last about 35 to 40 days at this rate of production. During the bloom period the assimilation was 5-9% of the supply and the amount available would last only 11 to 19 days if the high rate of production were maintained. During steady-state conditions the available supply would support the observed production for little over a month. Since the rate of production observed during the steady-state conditions persists throughout at least 5 months of the year it is clear that the processes of regeneration and vertical mixing, which have been discussed above, are vitally important in maintaining the general productivity of the sea.

When the requirement for phosphorus is related to the size of the standing crop of particulate matter the results indicate that the requirement ranges from 8 to nearly 50% of the standing crop for the observed daily rate of production. The time required to produce new organic matter equal to that present in the standing crop can also be derived from these values. This would be equivalent to a doubling time for the population if all of the newly produced organic matter remained in the population. Since the crop is continuously being grazed by herbivores and parts of the population are sinking to depths below the euphotic zone the increase in the standing crop is much less than the new organic matter formed.

At the start of the pre-bloom period, when the requirement is 49% of the size of the standing crop the population produces biomass equal to its own size in two days. Because of grazing and other losses, the population was observed to increase by only 33% in the five-day period between observations. At the start of the bloom, nine days would suffice to produce enough organic matter to double the size of the crop, but the observed increase was only 50% in the ten-day interval between observations. Most of the balance of the organic matter produced was found in the particulate matter in the deeper water. During steady-state conditions, a week would produce organic matter equal to that in the standing crop, but the actual change was a decrease in the surface layers and only a 3% increase for the water column as a whole for the five-day period.

These results demonstrate that the total annual production of organic matter in the marine environment requires more nutrient materials than can be found in the near-surface waters at any given time of the year. The observed rate of production must be maintained by the regeneration of nutrients in the biological cycle and by vertical mixing. Our results indicate that nearly half of the daily requirement for nutrients may be met by the regeneration of elements. The phytoplankton population has a very rapid turnover rate and the necessary nutrient elements are supplied by rapid recycling. Instead of a single crop during the year, as is typical of terrestrial communities, the oceanic population produces several crops during the year. The ratio between the available supply and the requirement for nutrients indicates a recycling six to ten times each year in our coastal waters.

Acknowledgements

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TABLE 1

THE SOURCES OF SUPPLY OF PHOSPHORUS UNDER THREE ENVIRONMENTAL CONDITIONS

	Pre-bloom	Bloom	Steady State
Total Phosphorus Cycle mg at/m^2/day	0.89	1.65	0.54
Source			
Removal, %	28	86	0*
Vertical mixing, %	72	12	57
Regeneration, %	0	2	43

* Inorganic phosphate increased in the euphotic zone by 0.22 mg at/m^2/day. This amount was also supplied by vertical mixing.

TABLE 2

FATE OF PHOSPHORUS ASSIMILATED IN THE PRODUCTION PROCESS UNDER THREE ENVIRONMENTAL CONDITIONS

	Pre-bloom	Bloom	Steady State
Total Phosphorus Cycle			
mg at/m^2/day	0.89	1.65	0.54
Remaining in Euphotic Zone			
mg at/m^2/day	0.19	0.90	0.40
As Particulate P, %	7	47	(-6)
As Dissolved Organic P, %	15	6	31
Regenerated, %	0	2	43
Found Below Euphotic Zone			
mg at/m^2/day	0.70	0.75	0.17
As Particulate P, %	6	45	9
As Dissolved Organic P, %	72	0	23

TABLE 3

THE RELATIONSHIP BETWEEN THE REQUIREMENT FOR PHOSPHORUS AND BOTH THE SUPPLY OF INORGANIC PHOSPHATE IN THE EUPHOTIC ZONE AND THE SIZE OF THE STANDING CROP.

	Pre-bloom		Bloom		Steady State	
Total Phosphorus Cycle mg at/m^2/day	0.89		1.65		0.54	
	Start	End	Start	End	Start	End
Inorganic P Supply mg at/m^2	35.4	32.9	31.7	17.5	19.7	20.8
Requirement, % of Supply	2.5	2.7	5.2	9.4	2.7	2.6
Days of Supply	40	35	19	11	36	38
Standing Crop (P) mg at/m^2	1.81	2.41	15.3	22.9	3.8	3.7
Requirement, % of Standing Crop	49	37	11	8	14	15

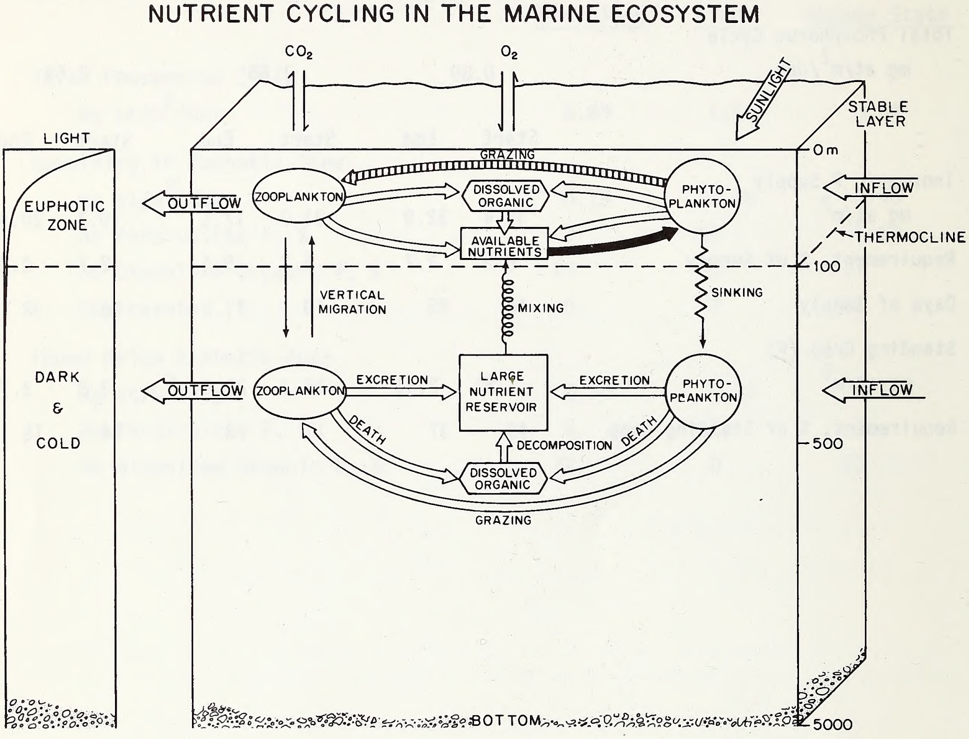

Figure 1 Nutrient cycling in the marine ecosystem, showing schematically the penetration of light into the sea, the major reservoirs for nutrient elements and the processes which transfer elements from one reservoir to another.

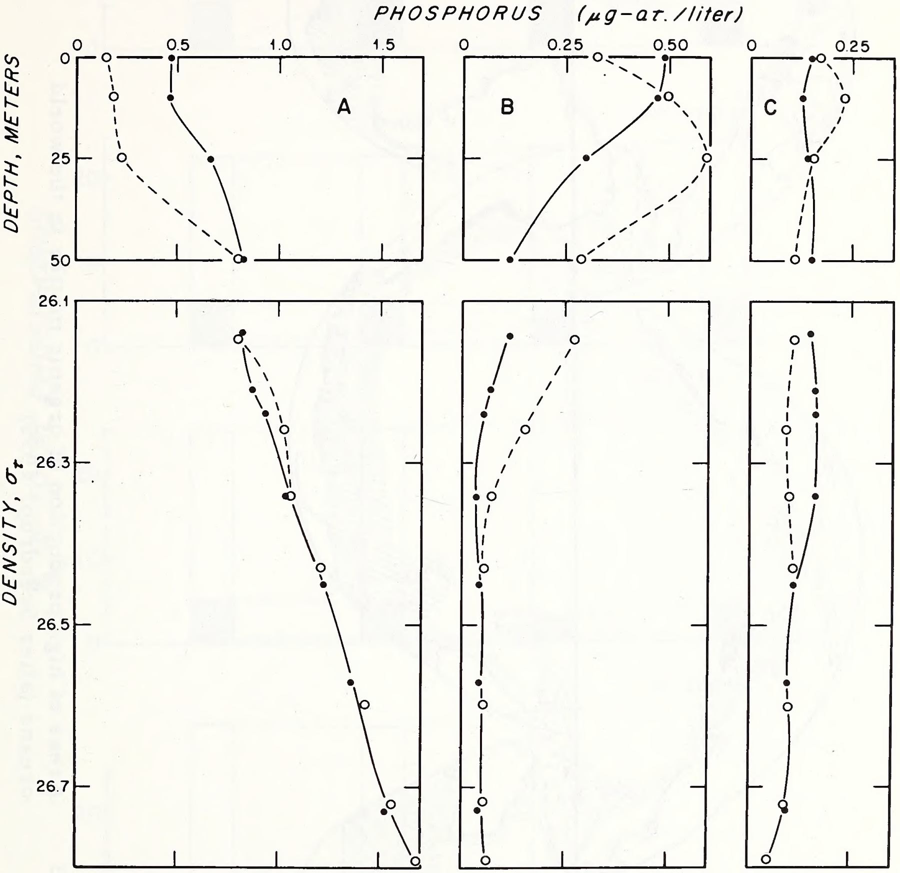

Figure 2 The phosphorus content of the waters of the Gulf of Maine at the beginning (solid line) and end (dashed line) of a ten day period in April 1964. The data are plotted as a function of depth from 0-50 m. and of density from 50-200 m. A: inorganic phosphate; B: particulate phosphorus and C: dissolved organic phosphorus. (Ketchum and Corwin, 1965).

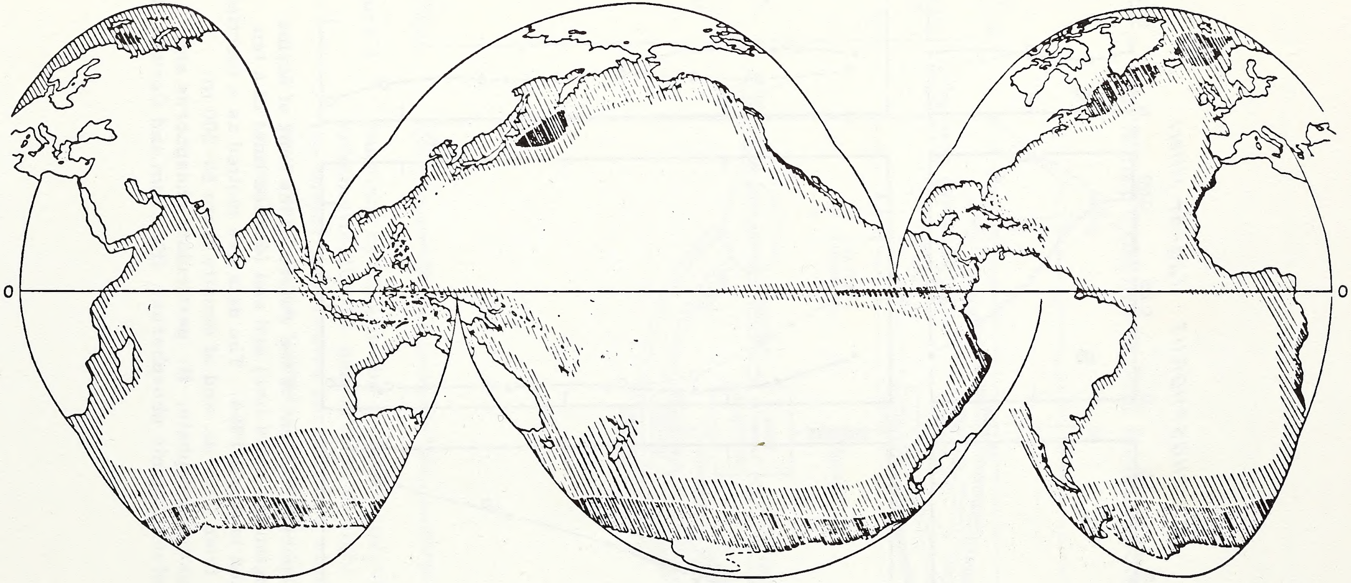

Figure 3 Areas of high production of organic matter in the world oceans (after Sverdrup, 1955).

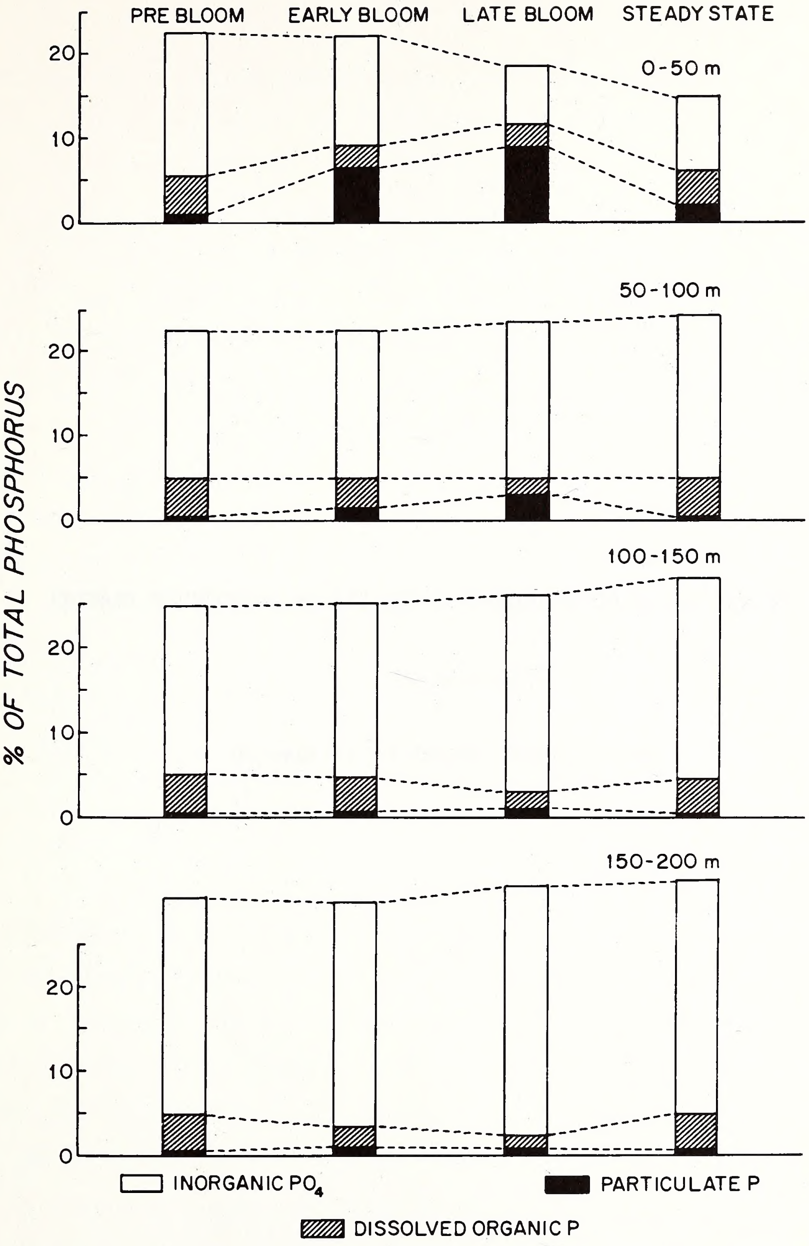

Figure 4 The distribution of phosphorus in the inorganic, dissolved organic and particulate fractions in four depth zones of the Gulf of Maine at different stages of the plankton cycle.

PRIMARY PRODUCTION RELATIONS IN WOODLANDS OF PINUS DENSIFLORA

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PRIMARY PRODUCTION RELATIONS IN WOODLANDS of PINUS DENSIFLORA[1]

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In Japan many studies have been made on biomass and production of woodlands of various types; following the author's paper on the production relations of Pinus densiflora plantations of different stand density (Senda et al 1952). Many papers have been published based on woodlands of Pinus densiflora (Satoo et all 1955, Sakaguchi et al 1955, Ando et al 1962, Hatiya et al 1965, 1966, Tochiaki and Hatiya 1966, Hatiya and Fujimori 1967, Hatiya and Tochiaki 1967, Kan and Shidei 1967, in which considerable data were accumulated, but most lack information about roots and almost all lack information about undergrowth. Because the measurement of increment in roots is very difficult and the measurement of increment in branches is very laborious, information on primary production is very limited. In this paper production relations are discussed with the estimation of biomass and production including roots and undergrowth of a young pine woodland along with published, as well as unpublished, data covering 67 woodlands from the Pacific side of eastern Japan.

1. Biomass

1-1. Tree layer

In a 15-year-old natural woodland, a sample plot of 4 x 5m was clear cut, and biomass was measured on all trees in the sample plot and summed. Biomass was compared with estimates of other methods which are very often used. Allometric relations of the dry weight of each part and whole tree were determined with all trees and with five trees selected to include the largest, the smallest, nearest to the mean cross-sectional area, and trees in between, as shown in Figure 1. With the equations and the frequency distribution of diameter of the plot at an interval of 1 cm, biomass per unit ground area was estimated. As a tree of mean cross-sectional area was not found in the plot, the dry weight of each part of such trees was estimated from the allometric relations with all trees, and the biomass per unit ground area was estimated by multiplying it by the number of trees. Biomass was also estimated by the ratio of the sum of the cross-sectional area of give selected trees to all the trees in the plot. As seen in Table 1, the deviation from the "real" value was not much for most of the values estimated by different methods. Stem biomass is presented in many yield tables, eliminating the need to discuss if here. Figure 2 shows the relation of the branch biomass to the age of woodlands. Branch biomass per unit ground area increased with age (r = 0.69), but there were some woodlands having exceptionally large branch biomass. Branch biomass per unit was influenced largely by stand density, among woodlands of the same age on similar sites. Woodlands with higher densities have smaller branch biomass, reflecting self-pruning. Some examples of this relation are shown in Figure 3. This trend was not true for leaf biomass. In Figure 4, the leaf biomass of many woodlands are shown in relation to age. From 4 to 46 years, leaf biomass seems to be independent of the age of woodlands, if the number of trees are large enough to make a closed stand. Figure 5 shows the relation between leaf biomass and density of experimental plots of 4, 5 and 13-year-old. Provided that the stand has density high enough to close, corresponding to the size of tree, leaf biomass was indenpendent of the stand density. It was previously reported that stand density did not affect the leaf biomass per unit ground area (Adams 1928, Moller 1945, Senda et al 1952, Satoo et al 1955, Senda & Satoo 1956.) Möller (1945) reported that leaf biomass of closed woodlands of European beech and Norway spruce was not influenced by factors such as stand density and site quality. The author (1966, 1967) reported that leaf biomass of closed stands of Cryptomeria japonia was influenced by site quality, though many other factors did not affect it. Figure 6 shows the relation between leaf biomass and site index which is presented as the ratio of mean height of the woodlands to the height of site class I in the corresponding yield tables. The relation was not as clear as in Cruptomeria plantations; the lower limit was similar for all site qualities though the upper limit increased with increase of site index. From the data shown in Figure 6, some groups of woodlands were selected and shown in Figure 7. Leaf biomass was dependent on site index for some groups, but in others variation within similar site index was large. Root biomass data is limited, however, as seen in Figure 8, root biomass increased with age (r = 0.93).

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[1] Contributions from JIBP-PT No. 18.

1-2 Undergrowth.

Biomass of undergrowth was measured in a 15-year-old woodland in December. Undergrowth biomass was small, but many species were present. In a plot of 20 sq m there were 264 plants belonging to 67 species, of which 33 were represented by a single plant. Mean dry weight of the plants was 2.3 g. Total biomass of undergrowth amounted to 314 kg/ha. This value is very small for a woodland of P. densiflora. Only one other bit of information is available about the biomass undergrowth in woodland of this species. A group of young woodlands near this stand had an average of 6.24 t/ha of undergrowth biomass. In mature woodlands of this species, a very thick shrub layer is usually found. However, no quantitative information is available.

1-3. Distribution.

The distribution of biomass into parts of the woodland of a 15-year-old stand is shown in Table 2. Of the total biomass, only 0.5% belonged to undergrowth. In the tree layer 83% was above-ground and 17% was underground. Using the same material as in Figure 8, the distribution pattern of the biomass into each part of tree layer is shown in Figure 9, as a function of age. The root percentage increased and the leaf and branch percentage decreased with age, although variation is rather large. This trend reflects the fact that the matter produced and distributed into the stem is accumulated year by year while the life span of leaf and branch parts is very short. Except for very young woodlands, the percentage of underground parts in the biomass was relatively stable throughout all ages for which data were available. From 13- through 46-years, the percentage of root biomass ranged from 16 to 18% (mean 17.1%) of the total biomass. If this stability could be generalized, this value could be used for the estimation of root biomass which is very laborious and difficult to obtain, but it may be too early to conclude. We need much more evidence.

2. Vertical distribution of biomass.

With vertical distribution and the extinction of light through the foliage, the production structure of ecosystems is clearly shown (Monsi & Saeki, 1953). The vertical distribution of biomass in the tree layer differed by stand density or state of competition, though the amount of leaf biomass itself was not affected, as shown by Figure 10. According to Monsi & Saeki, the relative light intensity (I/Io) in a certain depth of foliage is dependent on leaf area bove it (F) and described as

$$I/Io = e^{-KF}$$

where K is light extinction coefficient varying with species. This relation also holds true with the weight of leaves instead of leaf area which is very difficult to determine in conifers (Satoo, 1962). Figure 11 was prepared from Figure 10 to show this relation which is also clear for pine woodlands. However, the value of K varied with stand density and K was smaller in denser stands where branch biomass is smaller. This trend means that no only leaves, but also branches take part in the extinction of light in the crown canopy. To use the equation which was originally found for herbacious and grass communities in woodlands, it must include the light extinction coefficient of branches beside those of leaves.

3. Net production.

Net production of the 15-year-old woodland was measured by summing the dry matter production of each tree, and is shown in Table 3. The 15.8 t/ha amount is nearly the same as in a nearby plantation of Cinnamomum camphora with ample undergrowth (Satoo, 1968). Estimation of production of the undergrowth, which is supposed to be very small according to the biomass data, was not made because of technical difficulty. It was too small to make stem analyses, separation of the leaves of evergreen components by age was practically impossible, and the life span of the leaves of most are not yet known. In addition, the undergrowth of this woodland consisted of too many species to analyze separately.

There is very little data on the net production of woodlands of this species. There is a considerable amount of information on the production of stems and leaves, information on the production of branches is very limited, and there is no information on the production of underground parts, but the present work. Data on production are shown in Figure 12 in age sequence. No relation was recognized between net production and age of woodlands, and variation was rather large within age classes. Figure 13 shows the relation between net production and site index. No relation was recognized between net production and site index, except in one group. Hatiya et al (1966) reported that net production by a group of young woodlands of this species had close connection with tree height.

Distribution of net production into parts of woodland is shown by Table 3. Only about one-half of the net production was distributed in the stem which is the objective of forestry. Others may be considered as "production cost". The distribution pattern of the produced matter within the above-ground parts in woodlands was not dependent on age, as shown by Figure 14. The mean values of the distribution for 23 woodlands were, 50% to stem, 19% to branches, and 31% to leaves. The distribution pattern is dependent on factors other than age. Among factors affecting the distribution pattern of net production are stand density

(Satoo et al, 1955, Satoo, 1966) and site quality (Hatiya et al, 1966, Satoo, 1966).

4. Efficiency of leaves.

As net production (P) is a part of the product of photosynthesis, P can be divided into leaf biomass (F) and its efficiency (P/F) as

$$P = F \times (P/F).$$

Figure 15 shows the relation between the net production of trees in a 15-year-old woodland. The production of trees was almost linearly proportional to the leaf biomass on them, and is described as

$$P = 3.427\ F.$$

The net production per unit amount of leaf, or net assimilation rate in British terminology, was 3.427 g/g/year. For comparison with other data, the value for above-ground parts was calculated similaryly as 3.280 g/g/year. The assimilation rate can also be determined by dividing the value of net production per unit ground area with the corresponding leaf biomass, or as the mathematical mean of net assimilation rate of trees. Those values are also shown in Table 4. The values determined by different methods did not differ very much, if exceptionally large values of the smallest two trees, which do not contribute much to the production of the woodland are excluded from the calculation of the mathematical mean. The net assimilation rate of this woodland was 3.43-3.64 g/g/year or slightly less than 0.07 g/g/week. As no data are available for net production including underground parts, except this one, the relation between net production for above-ground parts (P') and leaf biomass (F) of woodlands is shown by Figure 16. Net production (above-ground only) per unit area was roughly proportional to the leaf biomass (r = 0.87), and shown as

$$P' = 1.823\ F.$$

Net assimilation rate (above-ground) was 1.823 g/g/year, or 0.035 g/g/week. The mathematical mean of net assimilation rate (above-ground) of these woodlands was 1.855 g/g/year, or 0.036 g/g/week which is not far from the value determined by means of the equation.

From Table 12 of Rutter (1957), who studied annual cycle of net assimilation rate of young *Pinus sylvestris* plants, the annual net assimilation rate during the fourth year of growth was calculated as about 2.54 g/g, or slightly less than 0.05 g/g/week. Considering the fall of net assimilation rate with age (Rutter, 1957) and the unfavorable photosynthetic conditions of leaves in closed stands, the value obtained here is very high. However, the leaf biomass of most of these woodlands was determined at its minimum. Most of the leaves of the older age classes were already shed after the end of growing season, and in the growing season when photosynthetic activity is very high the woodlands must have had much more leaves. The value of net assimilation rate throughout the year must be lower than these values. Therefore, it is necessary to trace the seasonal change of biomass.

As shown by Figure 15, the net production of trees within a woodland was closely dependent on the leaf biomass on them, but hardly on the net assimilation rate. This was also true for the production of woodland on net assimilation rate. A similar relationship was reported by Watson (1947) on mangold plants with varying fertilization. Satoo (1967) reported that stemwood production of *Cryptomeria japonica* woodlands was dependent both on leaf biomass and efficiency of leaves to produce stemwood. Hatiya et al (1966) suggests that net production by young woodlands of this species is depencent both on leaf biomass and net assimilation rate.

5. Gross production.

The loss of produced matter through respiration was tentatively calculated for the 15-year-old woodland. As the basis of calculation, the distribution of branches and stems of different age and size, mean monthly temperature at the observatory 5 km from the woodland, and respiration measured at 23°C with an infrared gas analyzer were used. Respiration was measured for leaves, branches of different sizes and age, and stems of different size and age up to 10 cm of diameter, and converted into the weight of carbohydrate by multiplying with 0.614. Respiration loss per year per hectare was 15.66 t for leaf, 6.99 t for branch, 10.38 t for stem, and 5.06 t for root, 38.09 t in total. With 15.78 t of annual net production, the gross production of the tree layer of this woodland was tentatively estimated as 53.87 t/ha/year, of which 71% was used for respiration, 15% was used for reproduction of crown and root system, and only 14% was accumulated in stem.

6. Summary.

Production relations were discussed with published as well as unpublished data, covering 67 woodlands of P. densiflora in eastern Japan. Methods of estimation of biomass were compared on a 15-year-old woodland. The deviation from the "real value", which was determined by clear cutting the plot, was not large in any of the methods used. Branch and root biomass increased with age of woodlands although the effect of stand density on branch biomass was large, but no relation was recognized between leaf biomass and age of the woodlands up to 46-years. Even 4-year-old stands had similar leaf biomass as mature woodlands, provided the number of trees is so large that stand is fully closed. The upper limit of leaf biomass in woodlands increased with increased site index, but the lower limit was not affected by it, although in some groups of woodlands it increased with increasing site index. The biomass of the undergrowth of the 15-year-old woodland was also described. With increased age of woodlands, the distribution of biomass in the stem increased and that of the branches and leaves decreased, but distribution in underground parts was fairly stable. The vertical distribution of the biomass in the woodland was influenced by stand density. For the extinction of light in the crown canopy, Monsi and Saeki's equation was apparently applicable for woodlands, but it was pointed out that is must be modified to include values for branches. Net production of the 15-year-old woodland was 15.8 t/ha/year which is similar to a nearby plantation of Cinnamomum camphora with ample undergrowth. Net production of woodlands was independent of age and had no clear relation with site index except for one group. Only one-half of the net production was distributed in the stem. Net production was dependent on leaf biomass but independent of net assimilation rate. The net assimilation rate of the 15-year-old woodland was 3.43-3.64 g/g/year and the mean value of net assimilation rate (above-ground only) of 23 woodlands was 1.82-1.86 g/g/year, though there is a reason to consider these values too large. Loss by respiration of the tree layer of the 15-year-old woodland was tentatively calculated as 38.09 t/ha/year as carbohydrate, and thus gross production was 53.9 t/ha/year, of which only 14% was accumulated in the stem of tree.

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* Jap. w. Engl. summ., ** Jap., *** German.

Table 1. Comparison of estimates of biomass by different methods.

method	1	2	(2/1)	3	(3/1)	4	(4/1)	5	(5/1)	(5/4)
leaf	4.565	4.965	1.087	4.371	0.965	5.000	1.095	4.798	1.051	0.960
branch	6.333	7.010	1.105	5.896	0.931	7.208	1.138	7.147	1.133	0.995
stem	41.903	43.354	1.035	43.485	1.038	42.451	1.012	43.121	1.029	1.016
aboveground*	52.800	55.326	1.048	55.752	1.056	54.659	1.035	55.093	1.043	1.026
aboveground**		56.313	1.066	54.372	1.029	54.665	1.035	59.017	1.118	1.079
stump	7.573	7.524	0.994	7.215	0.953	7.929	1.047	7.600	1.004	0.958
root	3.272									
tree layer*	63.645	65.770	1.033	63.241	0.993	65.866	1.035	66.683	1.051	1.012
tree layer**		71.184	1.103	65.572	1.030	66.036	1.038	64.600	1.013	0.978

* sum of estimates of each part.

** estimates with equations determined for sum of parts.

method: 1: sum of the values of all clear-cut trees. 2: allometric relation for all trees. 3: tree of mean cross-sectional area. 4: ratio of cross-sectional area. 5: allometric relation for selected sample trees.

Table 2 - Distribution of biomass

	biomass	distribution		
leaf	$4564^{\mathrm{kg/ha}}$	7%	9%	
branch	6333	10	12	
stem	41903	66	79	
aboveground	52800	83	100	
stump	7573	12	70	
root	3272	5	30	
underground	10845	17	100	
tree layer	63645	100		99.5%
undergrowth	314			0.5
total	63959			100

Table 3. Distribution of produced matter.

	Production	Distribution	
leaf	4242	27%	29%
branch	2728	17	19
stem	7495	48	52
above-ground	14465	92	100
stump	918	6	75
root	395	2	25
underground	1313	8	100
tree layer	15778	100	
undergrowth	+	+	

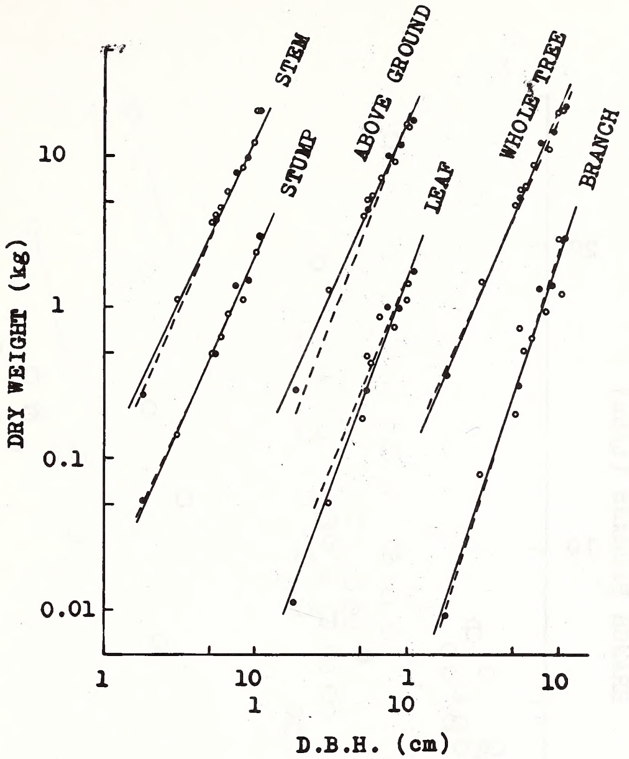

Figure 1. Allometric relations of dry weight of parts of trees to diameter. Broken lines were determined with trees indicated by filled circles; solid lines were determined with all trees, including those shown with filled circles.

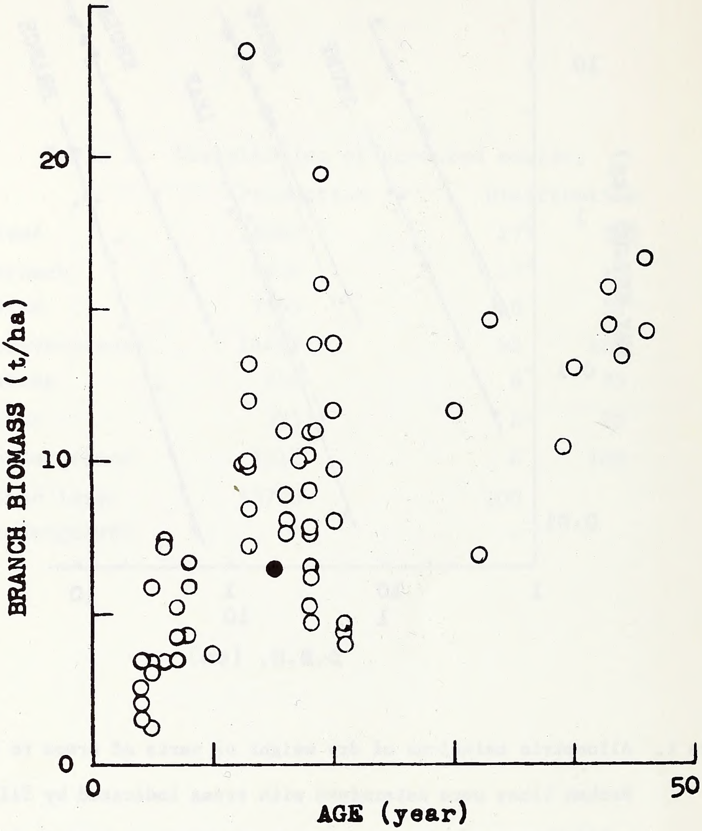

Figure 2. The relation between branch biomass and age of woodlands. The filled circle indicates the value for the woodland studied in detail (as in all the following figures).

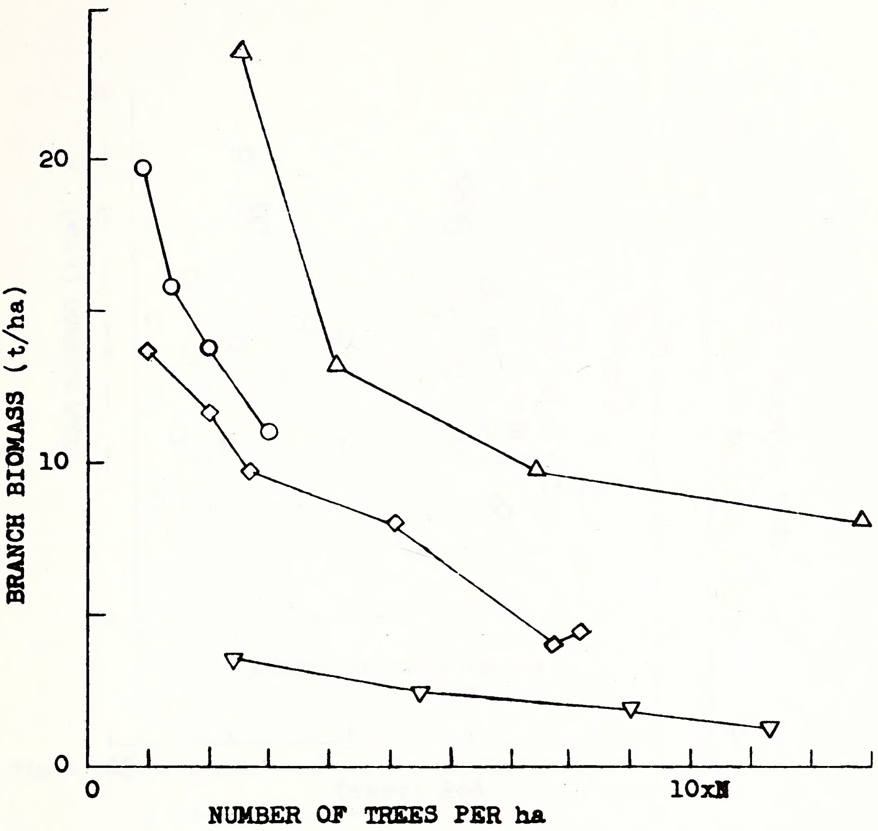

Figure 3. The relations between branch biomass and stand density.

▽ : 4-year-old, N = 10^5.

△ : 13-year-old, N = 10^3 (Senda et al 1952).

◇ : 20-21-year-old, N = 10^4 (Hatiya et al 1966).

○ : 37-year-old, N = 10^3.

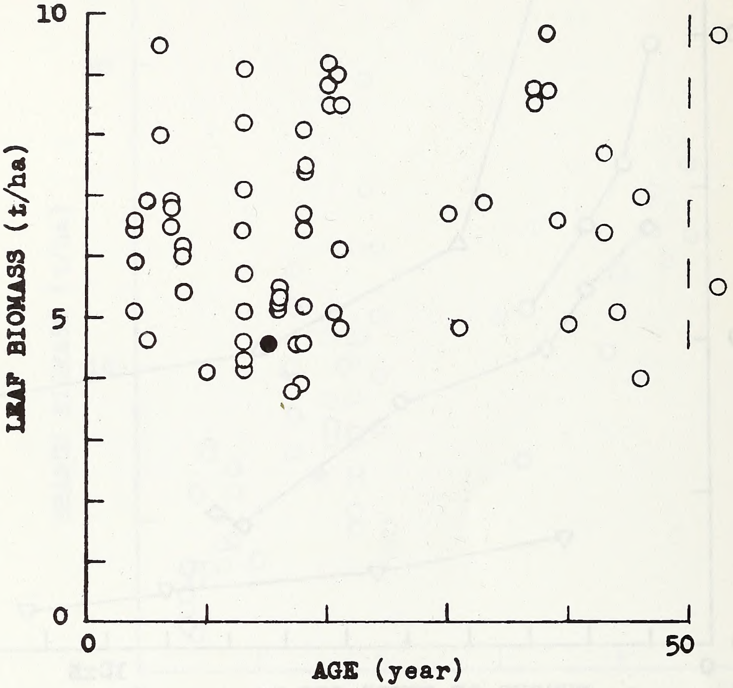

Figure 4. Leaf biomass (t/ha) in relation to the age of woodlands.

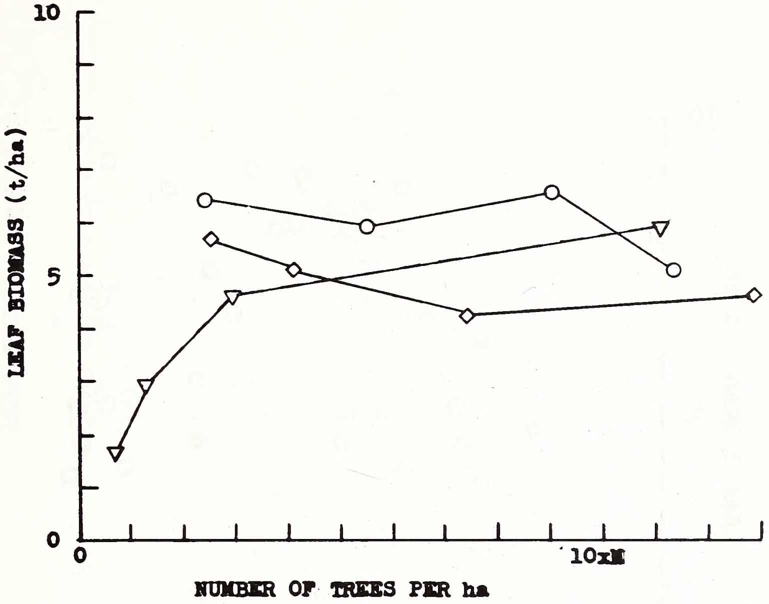

Figure 5. The relations between leaf biomass (t/ha) and stand density.

○ : 4-year-old, N = 10^5.

▽ : 5-year-old, N = 10^4, stands of lower densities are not yet closed.

◇ : 13-year-old, N = 10^3 (Senda et al 1952).

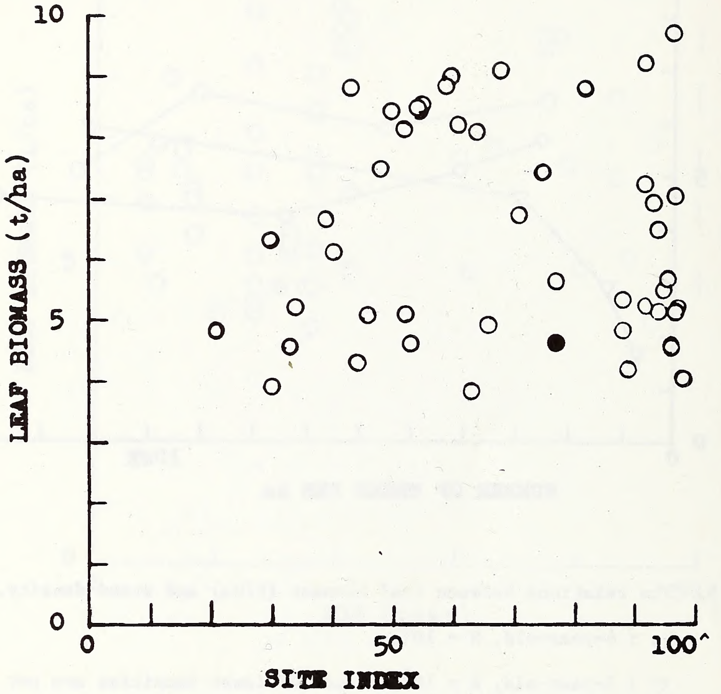

Figure 6. Leaf biomass (t/ha) in relation to site quality.

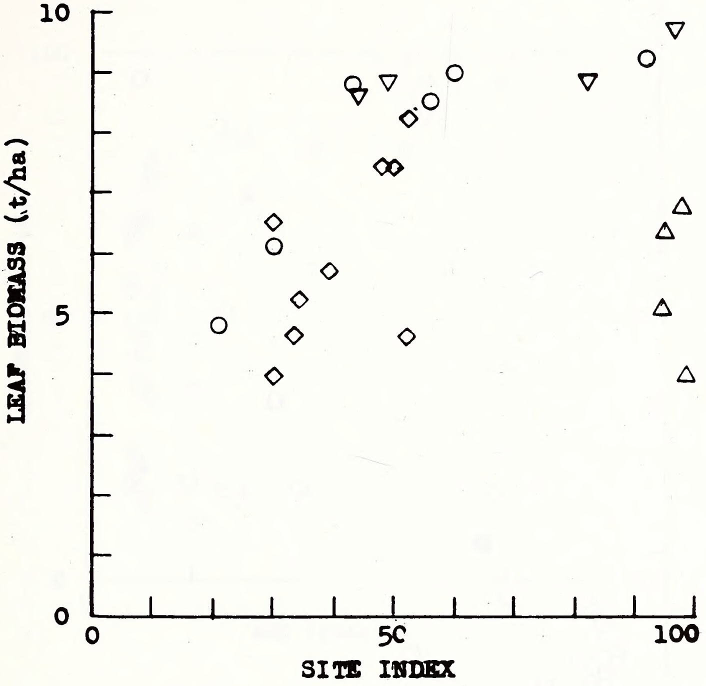

Figure 7. The relations between leaf biomass (t/ha) and site quality

◇ : 18-year-old, natural (Ando 1962).

○ : 20-21-year-old, natural (Hatiya et al 1966)

▽ : 37-38-year-old, planted

△ : 43-46-year-old, planted (Hatiya et al 1965)

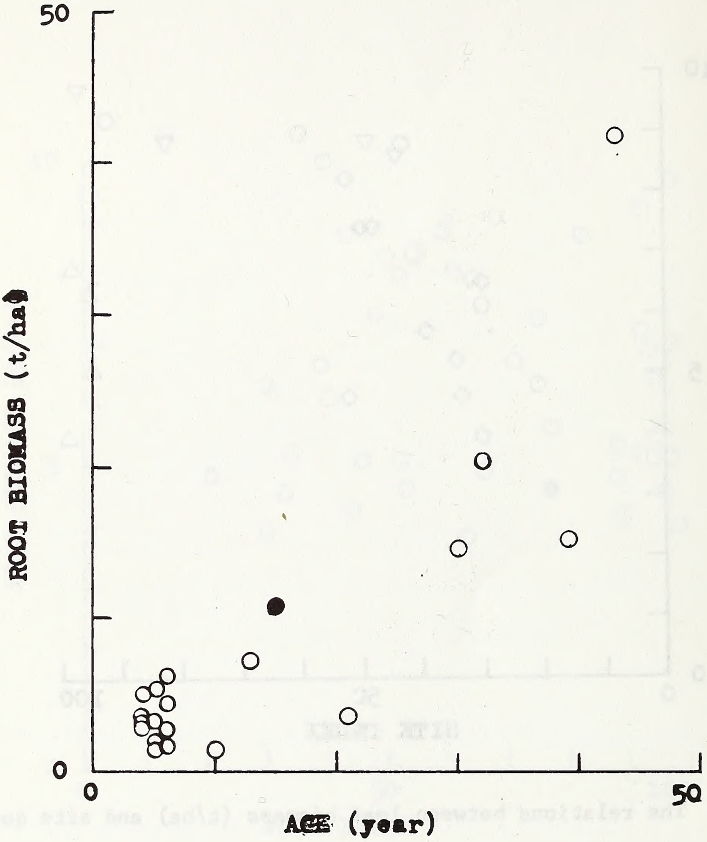

Figure 8. Root biomass (t/ha) in relation to age (years) of woodlands.

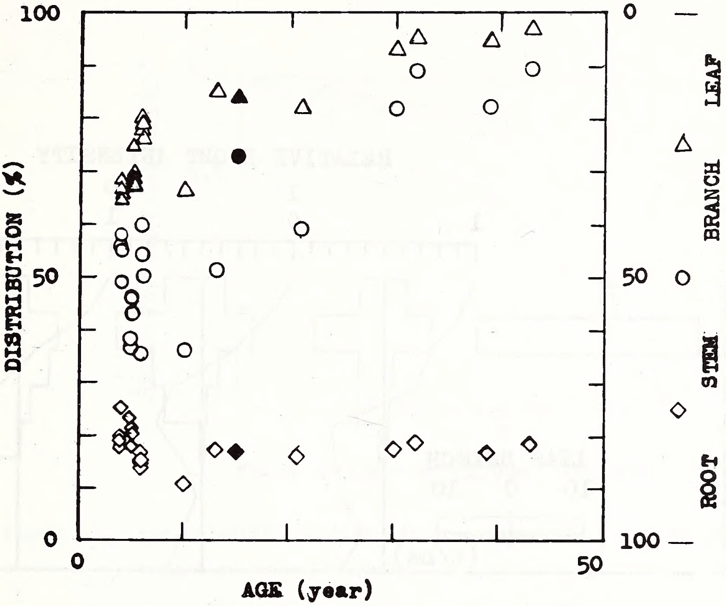

Figure 9. Distribution of biomass in the parts of trees in relation to the age of woodlands.

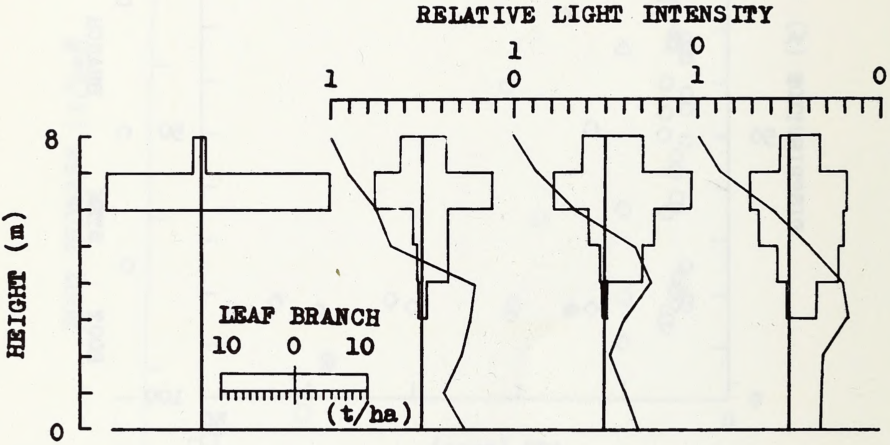

Figure 10. Productive structure of pine woodlands of different density, 16-year-old. Density is, from left to right, 12806, 7441, 4009, and 2462 trees per hestare.

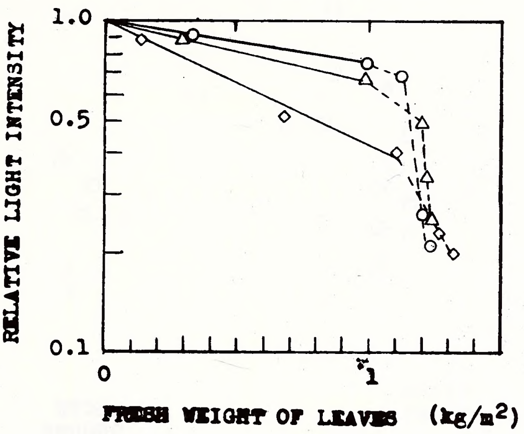

Figure 11. The relations between Relative Light Intensity and Fresh Height of Leaves (kg/m^2)

○ : 7441 trees per hectare, K = 0.2885
△ : 4011 trees per hectare, K = 0.4184
◇ : 2462 trees per hectare, K = 0.8414

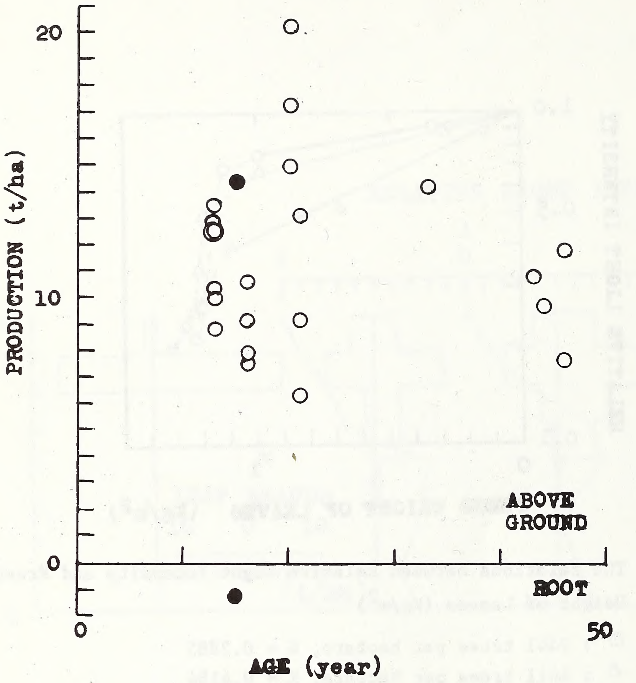

Figure 12. Net production in relation to age (year) of woodlands.

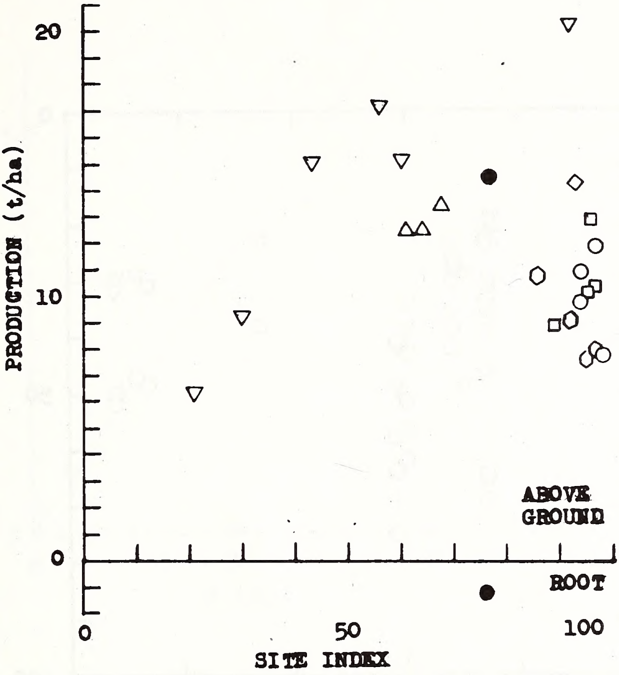

Figure 13. The relations between net production (t/ha) and site index.

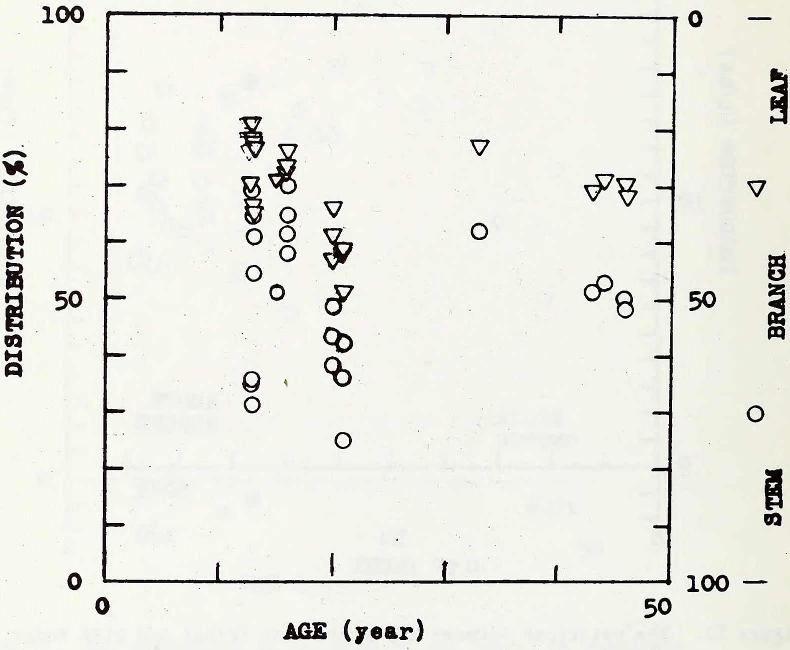

Figure 14. Distribution of net production (T/ha) in relation to age of woodlands.

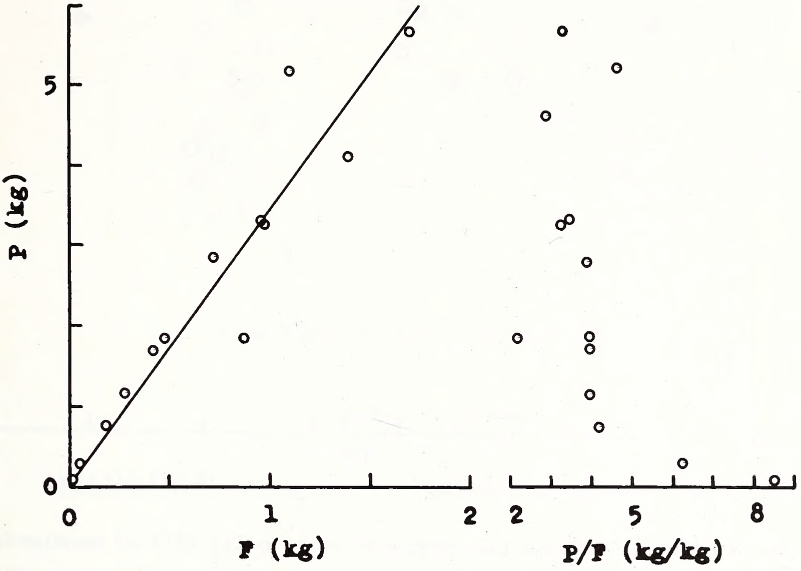

Figure 15. Net production of trees (P) in the woodland in relation to the leaf biomass (F) on them and to net assimilation rate (P/F).

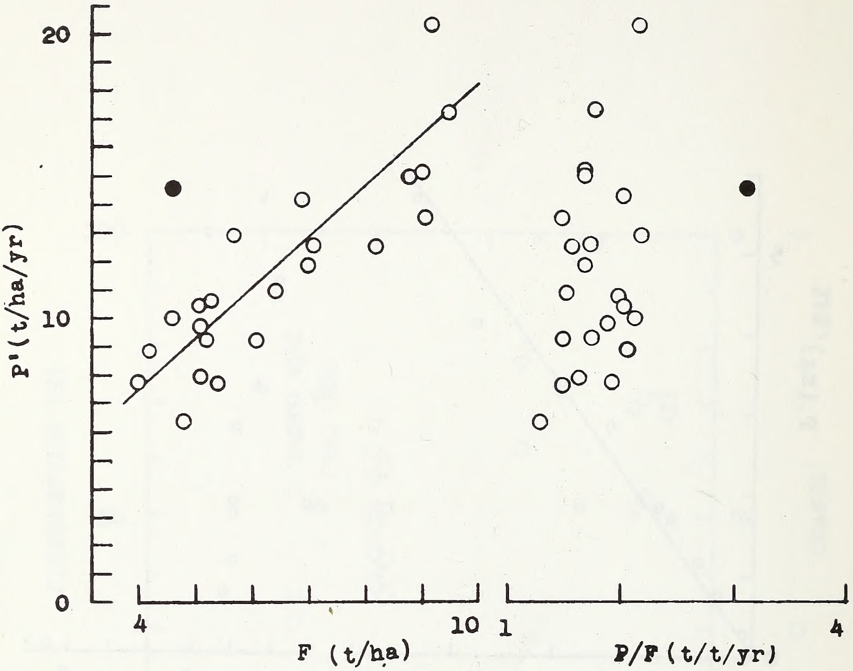

Figure 16. Net production (above-ground parts only) (P') of woodlands in relation to leaf biomass (F) and net assimilation rate (P'/F).

Table 4. Net assimilation rate.

Method	regression	P/ F	(P/F)/N	(P/F)/N*
Above-ground	3.280	3.169	3.744	3.281
Whole tree	3.427	3.521	4.215	3.642

* two exceptional values of suppressed trees were omitted.

P: net production per tree, f: leaf biomass per tree, N: number of trees.

WORK CIRCUITS AND SYSTEM STRESS

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ABSTRACT

Respiration of a compartment includes many essential flows of work which must be identified and measured separately for an adequate understanding of respiration of ecosystems. Using an energy-network language and the tropical rain forest as an example, efforts are made to identify some work flows, auxiliary energy sources, and diagram their relationships toward understanding forest energetics.

For example, the work flows in herbivore--plant pairs, serving as grazing control circuits, are evaluated from leaf hole data as 7% at steady state and more under disturbance. The growth rates of an exotic forest plantation are subtracted from climax gross production to estimate the energetic work cost of organizing rain forest species. Extending an old controversy, transpiration as a mineral pump in rain forests is considered as a principal limiting factor in adaptation of cloud forests with diminished forest height and proliferation of the small absorptive filter roots. The potential energy of dryness in in-flowing air is calculated as a fuel for night evapotranspiration and compared with the reversible heat changes. Turbulent eddy transfers are compared to food chains, and the optimum efficiency maximum power theorem is suggested to account for exponential properties of power spectra and the turbulent criteria of Reynolds number. A work circuit method of representing eddy diffusion pumping relates turbulence to auxiliary energy and limiting factor theories. The obligate nature of the optimum efficiency adjustments in making new work outlets is suggested for processes normally described as energy wasting. Stress is defined as an energy drain and the response of any stress becomes a reverse limiting factor hyperbola where flexible switching of energy reserves makes potential energy the ultimate limiting factor. Any limiting factor thus becomes definable as a fuel. Curves of response of systems to stress and curves of response of chemostats and other populations to drains of harvest turn out to be the same class of phenomena all involving a shift of position on the limiting factor hyperbola. The magnitude of work required to induce disorder is considered, an estimate being attempted for the ratio of gamma radiation disordering to reordering work of maintenance. Possibilities exist for comparing order-disorder ratios of such antagonistic microscale processes with macroscale processes such as the antagonism of disordering war against the maintenance of the structure of whole countries.

INTRODUCTION

It may be appropriate in a symposium on mineral cycling and energy flows to consider the role of flows of useful work using an energy circuit language previously introduced (Odum, 1967a, 1967b). Most studies of network mineral and energy flows have concerned main power flows of light and fuel energies passing successively from plants to microorganisms and animal trophic levels. The necessary useful work being done by the organisms in these networks has usually been included in the general category of respiration. Moving beyond the emphasis on the processes of productive biomass storage, we need to identify the respiration work flows and find ways of measurement.

Rain forests are among those systems with the most respiratory work (Odum, 1962; Odum, Copeland and Brown, 1963; Muller and Nielsen, 1965; Yoda, 1967). Consider some examples from the Puerto Rican rain forest to illustrate work flows and possible means for their evaluation. Ultimately, the energy circuit diagram for the flows of an ecosystem should have all the miscellaneous categories (i.e. respiration) replaced with as many flows circuit lines as there are separate real processes. For lack of knowledge and for simplicity, we separate out work flows in which we are interested and leave the others as miscellaneous respiration.

Energy Circuit Language

In Fig. 1 are some symbols of the modules of the energy circuit language. Each symbol represents a structure and a function with definite performance properties relating inputs and outputs. The energy network for an ecological situation includes lines for the regular flow of potential energy plus the work flows, some of which loop back from downstream energy sources to the upstream inflows, serving various roles there including control functions. The work control gate, for example, is a flow of work energy of one pathway which pumps and permits a second flow to pass over energy barriers. The kinetics of this module are given in Fig. 2 and the manner of its use is given in the abbreviated diagram of rain forest inputs in Fig. 3.

Classification of Work

Work is defined as the product of the force and the distance over which the force is exerted. One may classify the kinds of work involved in open systems into three types according to the nature of the forces involved in the work.

(1) Potential generating work is done in storing energy against a resting force so that the energy storage is a potential and from its storage are derived independent forces for driving other flows later. The elevation of water from the ground to the top of trees is work done against gravity. The incorporation of carbon-dioxide and water into glucose by photosynthesis is work against populations of molecular forces. When potential generating work is done at maximum power output, thus selecting the input-output loading for maximum rate of potential generating work, the efficiency is 50%, the other 50% going into entropy generating heat dispersal as a requirement of the second energy principle (Odum and Pinkerton, 1955; Tribus, 1961). Forces from potential generating work exist whether there is a velocity or acceleration or not.

(2) Frictional work processes are those in which work is done against the frictional forces that exist against a flow. The frictional force increases with the velocity. At steady state there is a balance between driving forces (from potential energy storages) and the frictional forces. Many of the work processes that are useful to an ecosystem are frictional such as flight of birds in air, the flow of water in tiny vascular elements of roots, or the flows of diffusion

in molecular systems of the cells. There are optimum rates of doing frictional work of useful and necessary types. Frictional work is less per unit flow at low speeds, but if flows are too slow the system is not competitive to alternatives with more rapid flows. If flow is too rapid, too large a fraction of energy passes into heat dispersal of the friction and the system is again uncompetitive.

(3) Acceleration work is work done against inertial forces so as to accelerate matter or charge. As in either the pendulum or induction coil, work may be recaptured essentially with 100% efficiency by decelerating the velocity into potential generating work. Such transformation is not really energy transformation subject to the degradation requirement of the second law of thermodynamics because it involves a velocity change from still potential energy to moving kinetic energy in our world reference that is a reverse change from moving state to rest in another world reference. As Einstein pointed out (1905) such inertial changes from still to moving states would appear just the reverse to a moving frame of reference and thus must be equal. Thus kinetic energy is really another kind of potential energy. If, however, the deceleration is done with frictional forces, the energy is dispersed as heat. Much of the necessary work of ecological systems consists of rearranging parts. Spatial organization requires acceleration and deceleration, the energy from the source passing into dispersed heat. Rearranging seeds, ants, or leaves may involve the work of arrangements thus involving acceleration and deceleration. As in the two previously discussed types of work, there is

an optimum rate. To accelerate faster increases the amount of potential energy dispersed into heat unnecessarily in braking, although some increased speed of organizational effort is achieved. To accelerate very slowly is to delay the time of achieving necessary organizational goals of system survival and to provide an edge to possible competitors.

Auxiliary Sources of Energy

In most ecological systems necessary useful work is done by more than one outside energy source. The light or the organic fuel inflow may be often identified as the main source of potential energy, but usually there are auxiliary inflows as well in which particular jobs which would have to be done by the system for itself from its storage reserves are instead done by the auxiliary flow facilitated by special adaptations of one or more organisms of the system. The kinetic energies of wind flow do much necessary work of circulating gases in forests, and currents in water move minerals and foods to sessile members of riffles and reefs. If an outside energy source provides the potential energy for pumping in a necessary limiting factor such as carbon-dioxide, it may be represented by the work gate symbol with the diagram in Fig. 2.

Work Gate Hyperbola

The kinetic behavior of the work gate module (Fig. 2) is that of the limiting factor hyperbola as has been derived or fitted in many sciences and various forms, often independantly. (Monod, 1942; Rashevshy, 1960; Ikusima, 1962; Caperon, 1967; Dugdale, 1968). The relationships in Fig. 1 are for a constant flow source. The local concentration of the limiting factor and its potential energy is maintained at x_1 by the steady flow J_a minus the utilization of the factor J_1 which is in stoichometric relationship to the main flow J as, for example, with the incorporation of carbon dioxide in photosynthesis. The main flow J depends on its driving population of forces of its main energy flow X_o according to conductivity of the flow L, but this conductivity is mediated by the driving impetus of the population of the local factor storage X_1, which in effect makes the flow a product of X_o and X_1 so that the multiplier "X" may be used in the diagramming symbol. As done in Fig. 2, the various relationships stated are written as equations and recombined to produce the familiar limiting factor hyperbola, which becomes a straight line if the reciprocals are plotted. The work gate module is an amplifier arrangement also and serves to represent the kinetics of chemical populations as well as ecological ones. (Sugita, 1962; Levine, 1966; Odum, 1967a).

Dry Air as an Auxiliary Fuel to Rain Forests

Drawing the limiting factor gate in the energy circuit language dramatizes the property of limiting factors as auxiliary fuels. An appropriate example in a symposium on system cycling is the limiting factor of unsaturated air required to pump evapotranspiration which involves water and mineral uptake. Holdridge (1947, 1962) might be cited among those who have suggested the importance of evapotranspiration in the morphology and productivity of rain forests. For example, a relationship between tree height and evaporation was cited from measurements by Tosi in Peru.

The opposite view that evapotranspiration is an unavoidable evil is given by Kramer (1959, p. 648) and Waggoner and Zelitch (1965). A number of summaries in recent years treat the energetics of evapotranspiration from plants (Deacon et al., 1958; Slatyer, 1963; Decker, 1965; Thornthwaite and Hare, 1965; Monteith, 1965; Gates, 1965; Briggs, 1967), but the essential role of potential energy controlling the process seems to have been missed in these energy budget discussions limited mainly to reversible heat changes. The potential energy from which the driving forces cause evaporation is in the water potential (Fig. 3) of the passing dry air and the coupling to insolation-induced heat-gradient potentials ($\Delta T/T$) especially in daytime.

Consider air capable of supporting evaporation therefore, in rain forest conditions where it may be limiting and thus serving as an auxiliary fuel. In Fig. 3 are drawn the energy flows involved in the main production of a rain forest. Note the role of wind as a limiting factor pump in providing a steady flow of air-bearing carbon-dioxide and evaporative abilities, both required in their turn as auxiliary energy drives to transpiration flow and to augment diffusion gradients to the photosynthetic process of leaves. Also included is a small flow by which the plant systems gate the leaf diffusion flows by control of stomata, in turn being controlled by guard cell responses to light.

The steady state removal of water by evapotranspiration is evaluated as the potential energy of a saturation deficit gradient whose energy value is the water potential, which is defined by the logarithm of the ratio of vapor pressures, the familiar expression of any free energy in terms of its molecular populations (Fig. 3, equation 2).

In the evaporative process even when it is, in theory, done reversibly without a gradient, there is a large heat absorption during evaporation (or release during condensation) due to the entropy changes of state associated with liquid and vapor states, the latter requiring more molecular kinetic energy. Often the latent heat of vaporization is computed as the total energy involved in evaporation of water from the Clausius-Clapeyron equation or its empirical evaluation. This procedure is only partly correct since the latent heat is only the reversible heat of the change of state. If only this amount of energy were supplied, no evaporation would occur since there would be no driving force, no gradient, no potential energy, and no irreversible heat, all of which are required for a spontaneous process according to the second energy principle. The relationships of the two energy components, the reversible heat change of state and the potential energy (free energy) capable of driving the process are summarized as equation (1) of Fig. 3. Substituting the logarithmic expression (1) for the potential energy and the latent heat expression for the reversible heat change, one obtains the total heat involvement in a steady state pattern of evaporation (Fig. 3). The large positive term for the reversible term (heat absorption) is partly cancelled by the negative term for free energy. Substituting values for the rain forest situation at El Verde, one finds the fuel energy available per gm is only -8.5 KCal.

The rate of potential energy consumption in evaporation may be divided by the rate of air exchange to obtain the fuel value of the wind to the transpiration process and thus its potential energy input to the ecological system work process. For the rain forest during the night of Feb. 24, 1966, for example, the leaves were dry and the observed evapotranspiration in a giant plastic cylinder was measured as 20 g/m^2/hr. when the relative humidity was 78%, the saturation deficit 6.0 millibars and the saturation vapor pressure 26.6 millibars (Odum, 1968). Potential energy in the form of ability to evaporate was being supplied at the rate of 0.170 KCal/m^2/hr.

Whereas and because the values of drying air as a fuel are small, they are contributing to useful work of the system to the extent that evapotranspiration is a useful part of the rain forest maintenance system. In other parts of the world the drying potential of the air is much greater, but is obviously serving not as an auxiliary fuel for the useful work of the systems survival, but in reverse as one of the climatic negative energy pumps (see below), against which special adaptation and expenditures are necessary. In either case the drying potential is a fuel, but the role as positive or negative energy flow varies as the property becomes in excess as in deserts. There it becomes work towards the potentials and processes of the atmospheric systems at the expense of the competing living systems.

When oxygen is abundant and food scarce, we regard food as the fuel. When, however, in the depths of a grain bin, food is in excess and oxygen is scarce, it becomes the fuel. Similarly, when energy or drying power and light energy are large in the desert, but water is scarce, the photosynthetic system is driven by water as one of the fuels. Walter thus graphs productivity in arid regions as a function of water (Walter, 1954). In the rain forest, however, with light and water abundant, the drying power becomes one of the fuels. Rosenzweig with MacArthur and McConnell(MacArthur and McConnell, 1966, p. 175) found a relation between net production and actual water evapotranspiration.

Transpiration as a Limiting Mineral Pump Affecting Morphology of Rain Forests

There is a loss of tree height with decrease in saturation deficit in rain forest climates throughout the world (Richards, 1952) that is well demonstrated with altitude on the slopes of small steep mountains such as El Yunque in Puerto Rico (Fig. 4), Cerro Azul, Panama, and Diablotin, Dominica. Although the rain does not diminish, the rain-forest belt with stauration deficit of 6 millibars gives way to a short scrub rain forest 40 feet high and then to the 12 foot elfin-mossy forest as the Saturation deficit approaches zero in almost continuous clouds in the condensation levels accentuated by orographic effects. Direct heating of leaves is diminished in shade, and relatively strong winds keep the leaf near air temperature. From these facts and from considerations of the very dilute nature of the surface soil waters of the leaching rain forest climate, one may postulate that unlike many other communities of the world, transpiration is a principle limiting factor accentuated by the dilution of the input minerals roots must provide to leaf photosynthesis.

Correlated with loss of height is the vast increase in numbers of small surface absorptive rootlets in the clouds (Fig. 4) as compared with the few water-trunk type roots found in lowlands where saturation deficits and transpiration rates are greater. Examples are given in Fig. 4. With loss of transpiration abilities the adaptation shifts to mechanisms of direct nutrient absorption and no longer can pull its minerals to great height. With these changes, the radioactivity accumulated in the forest from fallout increases as well, reflecting the greater role of actively absorbing roots and compression of living systems to a thinner layer than in the tall forests and deep soils of the lowlands.

A pigmy forest has been described in the mountain of California by Jenny (1960) and his pictures of thick surface root mat resemble the elfin forest of Puerto Rico (see also McMillan, 1956). The elfin forest does not occur where the regime in upslope clouds is intermittent as in parts of Costa Rica where the altitude for Elfin forest has oaks 150 feet high.

A calculation illustrates the dilution problem. Analysis of waters within the forest at El Verde show 0.0 to 1.0 ppm nitrate in through-fall and similar values in ground runnoff: The transpiration with the giant cylinder was measured as 1.3 mm and the daily leaf fall between 1 and 3 g dry matter/m^2, the leaves with 0.8 to 2.5% nitrogen before falling. Compare the rate needed to replace leaves and that obtained from the evapotranspiration on the assumption that water was pumped without concentrating the nutrients. Rate of transpiration supply if not concentrated is (0.1 mg/l N)(1.3 $l/m^2/day$) = 0.13 $mg/m^2/day$. Rate of nitrogen supply needed to replace leaf turnover is (1.0% N)(1.5 $g/m^2/day$) = 15 $mg/m^2/day$.

The calculation suggests the need could not be met by pumping soil solutions. Thus may be explained the observed preponderance of mycorrhizal-covered absorptive roots as a mat over the surface, the roots invading fallen litter and logs with the opportunity of short-stopping and concentrating critical minerals such as nitrogen before they become a part of the soil water or runoff.

It was reasoned by early students of the rain forest that transpiration is limiting mineral transport and that general forest adaptations to increase the wind, convection, and transpiration had helped to maintain an adequate upward transport where humidities were high and winds light: This view continues to be offered by many considering the whole forest system (Eyre, 1963; Winneberger, 1958). The theory was attacked by a generation of teleology-denying, anti-darwinian experimentalists who tested adapted rain forest plants to find transpiration limits. This was like looking for fish that can't swim and not finding them concluding that fins are not important for swimming. An earlier generation of teachers fighting excessive speculation ghosts of an even earlier era taught a dogma of denying that the physiological mechanisms and morphological patterns of plants had been controlled in prior selective cause by the reward requirements of the larger system network. Richards (1952) quoting McLean in part accepted this verdict on transpiration in rain forest. They, in effect, denied the existence of self-designing mechanisms above the physiological level of organization.

Discussing ordinary forests, Crafts, Currier, and Stocking (1949: p. 179) in a review statement acknowledged there was enough experimental work to say that transpiration "facilitates the distribution of minerals", but they concluded that transpiration was usually in excess. Ten years later Kramer (1959: p. 648) summarized evapotranspiration as an "unavoidable evil" without mentioning mineral cycling role. Those who deal with heavily fertilized agricultural crops or vegetation of arid lands are used to a concept of transpiration having little role as a mineral pump and certainly not being the limiting factor. From such backgrounds come the ideas to save water on watersheds by chemical treatment for closing of stomata (Waggoner and Zelitch, 1965).

For rain forests, however, we return now to consider the earlier view that the following properties of rain forests in addition to other roles they may serve, provide the following services to transpiration mineral pumping that might otherwise be limiting:

(1) Ragged crown and emergents to help develop eddies, although this property is diminished in hurricane belts.

(2) Leaf patterning to open holes and allow sunflecks so that more infrared insolation can reach and heat the forest floor from the bottom to help avoid stratification. The high infrared reflectivity of the leaves throughout the forest helps to get this insolation to the floor.

(3) The leaf form of such trees as the palms are constructed to

be unstable in weak forest breezes so as to flutter.

(4) The broad leaves increase the surface and evaporative power where saturation gradients and wind velocities are small.

(5) The drip tips and waxy surfaces serve to get more of the water to the forest floor and diminish the evaporation on the broad leaves (over 1/3 at El Verde), this also helping to get the minerals to the absorptive surface roots.

Based on the low transpiration rates found in the rain forest at El Verde, the pattern of increasing root numbers and diminishing tree height relative to air saturation deficit in rain forest mountain comparisons (Fig. 4), the calculation of considerable potential energies of the inflowing air as a fuel for drying, and review of the older evidences from others concerning evapotranspiration pumping in rain forests, this author concludes that transpiration-mineral pumping factors control morphology in rain forest ecosystems.

The question may also arise as to the amount of the transpired water which stops in the leaves bound into organic matter as part of photosynthesis. The photosynthetic rate of about 16 g carbon/m^2/day was obtained in giant cylinder measurements where night respiration (taken equal to day photosynthesis) was 7.7 gc/m^2/night and also obtained by summing the photosynthesis measured for single leaves using the leaf area index measured. The weight of hydrogen involved in ratio to this much carbon processing in organic matter was about 1.1 gH/m^2/day, whereas the amount of transpiration of water was 1300 g H_2O/m^2/day, a vastly greater flux of hydrogen (145 g H/m^2/day).

Consider also the amount of carbon-dioxide that could come up through the root systems where waters very acid from respiratory carbon-dioxide are being transpired. Even if there were 100 ppm free carbon-dioxide, and it were all passed in with the water, the amount reaching the leaves would be only that in 1.3 liters or only 0.04 g Carbon/m^2/day a negligible contribution to the known photosynthetic requirement.

Work Circuit for Eddy Diffusion Pumping

Consider the wind's role in the energy circuit flows drawn in Fig. 3. The diffusive spread of a population of chemical molecules is often described by the Fick diffusion law in various forms, the flux being proportional to the gradient of concentration according to a conductivity property of the pathway. Where diffusion is molecular, the spread of the molecules along the gradient follows the driving force of the gradient that is derived from the potential energy of the gradient; and after diffusion has equalized concentrations, the potential energy has become the dispersed heat associated with increased entropy as diagrammed in Fig. 5 (Best and Hearon, 1960).

Usually, however, the diffusion is not molecular and receives an assist from other energy flows which serve as pumps, their potential energies dispersing in heat so as to accelerate the spread of the chemical substance along its gradient. The spreading process is proportional to the gradient as in molecular diffusion but is much faster. Often one indicates this rapid property by indicating that the diffusion coefficient is larger. Often the so called constant is graphed with time and space as a variable which it thus turns out to be. In some fields one uses the analog language of the electrical circuits to say that the conductivity of the diffusion has increased and its reciprocal resistance has decreased (Fig. 1B). These ways of representing the flow involve misuse of constants as variables. The diffusion "constant" of resistance is really subject to forcing functions from second energy flows and not a constant. One may also indicate that there are two coupled processes each with terms that relate their driving forces to both fluxes. Actual electrical analogs have been used, some with passive and constant conductance (resistor) and some with energy pumping by operational amplifiers (Karplus and Adler, 1956; Brock, 1962). For ecological energy circuits, there may be some advantage in expressing the energy relationships more clearly with network diagramming symbols of Fig. 1 so as to show that the conductivity is proportional to the pumping work of a second flow. The relationship then may become a regular limiting factor hyperbola (Fig. 2).

Eddy Transfer of Momentum as an Energy Circuit

In prior papers efficiencies of food chains have been related to natural selection from competing populations that may produce an optimum power transfer. Any efficiency too large would be too slow and any efficiency too small would generate too little power transfer. Natural selection for maximum power thus adjusts the system to a characteristic decline in energies down a chain of transformations, the pattern being that capable of transfering maximum power and thus predominating over competing systems.

The fields of eddies in the atmosphere like living populations have many alternatives and continual reproduction of variety from which combinations can be naturally selected for maximum power dispersion, delivery, and ability to drain energies away from alternatives.

In many ways these chains of momentum transfer have properties of food chains. Building on concepts of Kolmogoroff after Blakadar (1955) one may consider the transfer of energy from large eddies to smaller eddies and ultimately to molecular motion, dispersing the potential energy stored in kinetic motion ultimately into heat. These authors showed that the ratios of eddies giving energy to those receiving it tended to develop in certain ratios so that the percent efficiency of change of energy tended to be similar at each transfer. MacCready (1953) for example found that there was a spectrum of turbulence which was logarithmic.

In Fig. 5 are diagrammed the energy circuits for a chain of eddies which may be in steady state receiving momentum input on the left and transmitting power to the right, dispersing some into unusable heat at each stage. With the decline in power the dimensions of the eddies decrease providing the logarithmic spectrum observed in eddy fields as in ecological chains.

Power Spectra and the Optimum Efficiency Maximum Power Principle

Although the observed patterns of energy decay in eddies fit concepts of momentum transfer in proportion to contained inertia, they require a more fundamental explanation in terms of energetics here proposed. Just as the optimum efficiency maximum power selection (Odum and Pinkerton,

1955) provides for particular decays of energy through food chains, so the observed similar percentages of energy transfer through successive eddy transfers may find a similar explanation. A 50% dispersal as heat may be the required entropy tax for maximum power effect on survival of systems. To the extent that there is potential generating work done by one eddy in generating a second, there may be the entropy tax adjustment for maximum power output.

A 50% transmission may be predicted for each eddy transformation where no other processes are involved. However, where there are other drains as with leaf drag in the forest, part of the energies are lost as work of the ecological system in friction. The drag of the leaves is an output of useful work from the point of view of the living forest system since the energy dispersed as heat in leaf friction is the same energy that renews and steepens the diffusion shells at the stomatal surfaces.

Obligate Power Dispersal and Entropy Generation Rates

It is a property of convectional development of cumulus clouds over a plain on a summer day, of forest fires (Graham, 1955) and of heat upcurrents over new volcanoes (Thorarinsson and Vonnegut, 1964) that rapidly developed potential energies in the form of heat gradients generate large scale convection systems that transfer away the energy much more rapidly than would be possible with ordinary or small scale eddy diffusion. Thus the incidence of dust devils, large cumulus circulations, and tornado spirals over sources of intense heat increases with temperature gradient. One may regard the development of the large eddies as a selection for maximum power transfer which drains away energies from the source in competition with the smaller eddies and molecular diffusion. We may use such evidence as indication that unless one spends special control energies to prevent choice-selection process, one cannot have a system which disperses energy at less than the maximum rate. Chains of energy transfer are limited in not being able to exceed certain efficiencies, because this would eliminate them in competition as too slow. They are also limited if their efficiencies are too small as this would allow energies to accumulate locally developing greater potential energy gradients, accelerating the selective value of the larger eddy systems.

The transfer of food down the food chains from a point source is similarly a series of energy eddies whose influence and cascade of declining effect is likely to be in the same proportion in each stage and thus logarithmic. The frequency diagram of energy dimensions of ecological components and the frequency diagram of eddy structure are likely to be similar. Maximum power dispersal may be considered obligate. Although one may set up a system that seems to waste potential energy according to the point of view of the man setting up the system, the overall process will not waste power but will transfer large energies into pumping processes as eddy chains thus doing work on the atmosphere instead of in the system being considered. A short circuit or forest fire may seem to be a loss of potential energy into heat, but changes in insulation and atmospheric structure result.

The Reynolds number is the ratio of the inertial force to frictional force in a fluid flow, and with increase in Reynolds number laminar flow changes to turbulent eddy flows. One may propose that there is selection for maximum power transfer. As long as one has potential energy in the form of kinetic energy flows and gyrals without any drain of energy into heat, one has no energy transformation. If one attempts to increase the energy drain into heat by increasing friction, one creates an energy transformation situation in which the transfer is at lower efficiency than the optimum, whereupon natural selection picks the larger dimensional eddies because the power transfer is selected for the maximum. The Reynolds number criteria for turbulence may thus be another means of stating the optimum efficiency maximum power principle and explained by it.

For eddies in water Leopold and Langbein (1962) have indicated the action of river systems in doing erosion work as in development of meanders in order to reduce the rate of generation of entropy. This may be only half of the story. If the gradient for energy transfer is aimed too rapidly into heat dispersal, the loadings are selected for more energy transfer into work and high grade energy storages such as rotary motions. On the other hand if loadings are too great, too little power flows, and competitive systems draw more power, do more work towards their own persistence such as cutting and transporting sediment. Streams that do cutting work steal from those that don't. Rather than Prigogine and Wiaume's (1946) statement of trend towards minimum entropy generation, the optimum efficiency maximum power principle suggests an intermediate adjustment. The minimum entropy generation is no generation at the reversible state, which is noncompetitive. Living and non-living flows which permit choice and selection evolve through their work expenditures towards the flow that allows the optimum efficiency maximum power adjustment. In streams the chain of constant percentage energy transfer may produce evolution of a logarithmic profile as discussed by Leopold and Langbein.

The phrase "work will out" may be useful in making the hypothesis clear that potential energy cannot be dispersed into heat without doing work of optimum power adjustment any more than work can be done without the tax of some into heat. Both are obligate. Prigogine and Wiaume's idea of minimum entropy may apply only to generation rates higher than the steady state competitive adjustment. For systems that are started with too small an entropy generation rate, the shift is towards higher entropy generation rates as suggested by Sugita (1951) in a statement of maximizing of entropy generation rate. The statements of trend to minimum and maximum rates are both half truths. The suggestions of Leopold and Langbein concerning geomorphologic evolution also seem more appropriate to the optimum efficiency maximum power hypothesis.

WORK CIRCUITS FROM SYSTEM ENERGY POOLS

So far the discussion has concerned the work flows by which outside auxiliary energy flows may control the main power flow of such systems as the rain forest. Many of the work flows, however, derive their energies from the system's own accumulated energy storages downstream in the circuit. In Fig. 6 are some of the workflows in the rain forest system. The energies involved in mycorrhiza are part of this work expenditure. The microorganisms decomposing leaf litter drain energy from the pool of old plant tissue already released from the living photosynthetic flows, and thus the drain has no upstream effect on the plant populations. Some insects also use food chain energies to pay for their work roles. How can such work flows be evaluated as to their calorie flow rates?

Grazing Control Circuit

The difficulty of evaluating work circuits is illustrated by the grazing control mechanism of the rain forest leaf herbivores in Fig. 6. Notice that the drain for support of the herbivorous insects is from the live, photosynthetic structures so that the action on these storages is negative. However, by providing a population of consumers that can grow in numbers in response to an increase in the population of suitable leaf tissue food, the herbivores serve as a grazing control mechanism. The biochemical specialization in the rain forest provides a different chemical matrix in most plant species--a resin--a pigment--a poison--etc., so that a consumer must have biochemical specialization to eat that plant species. With many biochemical specializations provided, the pairs of plant-host pairs is large and the distance between one tree and another that can be eaten is large. With the gauntlet of the general purpose reptile, amphibian, and bird consumers (Fig. 7) the probabilities of epidemic consumption are small except if and when one of the plant species gets more numerous than its normal proportion. Then its insect control agent can cut back its stocks to its steady state proportion. The roles of specialized chemical characteristics of species and insect adaptations find a common explanation. The principle emphasized by Vouté (1946,1964) that complex climax forests have stabilized insect populations thus finds explanation in biochemical specialization and the insulations for multiple grazing control actions.

In the El Verde rain forest, the leaf holes in falling leaves showed about 7% consumed by leaf grazers (Odum and Ruiz-reyes, 1968). After disturbance of a radiation stress the holes increased to about 15% but not as much as the 50% or more found by Woodwell in chronic radiation of a simpler forest at Brookhaven. These percentages may be used to estimate the part of the work circuit costs of the grazing control work due to the insect mechanism. From the circuit in Fig. 6, we may regard the idea of cost in two parts:

(1) A regular cost is the energy flow required to maintain the machinery that will do the regulation when it is needed. In the insect case this is evaluated from leaf holes as the fuel flow of 7% of leaf fall when the forest is near its stable structure and not being restored to steady state from some deviation.

(2) Additional cost is the energy flow of the regulatory work itself, not counting the energy required to maintain the machinery. In the grazing control action that followed irradiation this was an 8% additional energy drain required to prevent epidemic disordering of the forest system during recovery. This amount of energy might be supplied by an outside controlling agent such as man with a chemical spray, and he might well use more than this amount of energy in doing the control work. The actual value of the service, however, should be the energy cost when done in the most economical way. When leaf fall is about 1.5 $g/m^2/day$, with calorie values of about 4.5 Kcal/gm, the cost of the 7% grazing control insects

may be about 0.47 kCal/m^2/day and the cost of the grazing control action under radiation stressed circumstances an additional 0.54 KCal/m^2/day. Depending on the disturbance, therefore, the amount of calories remaining for the microbes for remineralizing energies from leaf source was between 85 and 93% of the leaf fall plus that received down the phloem from the tree.

Flexible Switching Makes Energy a Limiting Factor

The switching of energy reserves from one flow to another illustrated by the grazing control and mineral cycling flows is a general property of complex ecological and social networks with their branching and looping power and work flows. Ancient complex systems like the rain forest thus have means for diverting energy from some system pool into whatever factor may be limiting, whether it be pumping in a limiting material, or circumventing some negative energy draining work of the environment such as radiation. For those systems in which there are means for switching energy reserves to eliminate whichever factor is limiting, energy may be said to be limiting. Any other factor is eliminated by the energy reserves. This principle that complex systems usually have all limiting factors reducible to the one limiting factor of energy allows the energy reception module (Fig. 1) to serve not only in relating the performance of single chloroplasts, but also for whole systems of the cell, the tree, and the ecosystem generally. Consider, thus the energy receptor module, its kinetics, and the effect of energy input on system output where limits are in the energy itself and its own limitations in overcoming inherent costs of recycling of minerals and distributing work.

Fig. 7 shows the energy diagrams for three limiting factor gates that are supplied and controlled from outside auxiliary sources in (A) but are supplied from loopbacks of system pools in (B). Fig. 7C shows the hexagonal module which abbreviates the circuits in (B) where the main energy source is a fuel (potential energy accompanied matter flow). To receive pure energy flows such as light, sound, and water wave energies, a cycling receptor mechanism is required. This module responds with a logistic growth form with time (Odum, 1962a, 1967a) and has a transfer function in relation to strength of energy source that is hyperbolic like that of the outside limiting factor control.

The Hyperbolic Energy Reception Module

The hyperbolic relationship of a recycling receiver system has now been independently discovered and used in many sciences so that it is time we start considering it a general system theorem. A general statement is given in Fig. 8. For example, this module has been derived for enzyme substrate reactions (Michaelis and Menton, 1913; and Lineweaver and Burk, 1934), photochemistry (Mitchell and Zemansky, 1934), and photosynthesis of Hill reaction (Lumry and Reiske, 1959).

From the general form of the expression in Fig. 8 it is clear that the kinetics apply to any situation where there is a cycling receptor reacting with an input energy flow such as wave action in tide pools, cheap energy sources and dollar capital, or light energy on an ecosystem with cycling materials including chlorophyll, enzymes, and minerals.

The cycling receptor material such as chlorophyll (Q in Fig. 8) is distributed between a low energy state (Q_1) and a high energy state (Q_2).

The total quantity of receiving material is the sum of that in the two reservoirs and thus is limited. The rate of flow of low energy receptor to high energy state is a product of the input energy and the available receptor (product of two forcing populations). The return flow is proportional to the drive from the reservoir population of energized receptor, the return flow depending on the coupled work load. The above verbal statements are set out with the equations in Fig. 8 and combined to form the rectangular hyperbola. In B the circuits and kinetics in A are symbolized with the bullet-shaped energy receiver symbol. In C is the electrical circuit of a photometer which is one example, the electrons being the cycling material (Q). The transfer function of the module is graphed in 8D.

Hyperbolic Energy Function Recordings in a Rain Forest

The electrical circuit in Fig. 8C automatically calculates the output according to the hyperbola equation of A as drawn in (B). The separate leaves of a forest (as well as the forest as a whole) have this response as long ago established for photosynthesis of all kinds of plant tissues. Thus it may be a useful instrumental measurement to record the hyperbolic function as simulated photosynthesis, which includes the effect of light loading, but not the additional limitations that might develop with other complexities in the natural system. Hyperbolic function may be regarded as potential photosynthesis. In Fig. 9 are given some daily records of solar cells loaded with 5000 ohm resistors recording on the tower above the rain forest and also from the forest floor where a ring of cells was connected. Whereas regular light readings from moment to moment in forests show extreme ranges, the response of the hyperbolic receiving function has a much smaller amplitude with much more steady input to biological synthesis and maintenance procedures than might have been immediately obvious from the range of flickering light. The cyclic circuit of the receptor is a form of feedback stabilization of loading.

Optimum Efficiency for Maximum Power in Photosynthesis

In an earlier derivation of the principle of optimum efficiency and maximum power (Odum and Pinkerton, 1955, Odum, 1963) the details of the application to photosynthesis were not spelled out, although the behavior of a cycling receptor analogy, the "cannon ball catcher" was later discussed (Odum, McConnell and Abbott, 1959). The usual pattern in photosynthesis is a varying input and a more steady output load just reverse from the derivation in which the input was held constant and the output loading varied. In Fig. 10 are given the calculated theoretical efficiencies for the hyperbolic receiver system where the input is varied. The theoretical efficiency curve has the familiar shape reported from experimental papers on photosynthesis in the laboratory (Lumry and Spikes, 1957) and in nature (Edwards and Owens, 1962) to mention two of hundreds. The maximum power delivery point (encircled) occurs in the middle of the pattern, and any selection for maximum power may adjust the amount of cycling receptor material so that the loading is in the vicinity of the optimum efficiency point. The cycling receptor system provides a much smaller deviation from the optimum loading than would be provided without a recycling material. The mechanism allows excess energies to pass unabsorbed to other receptor systems below. Hence some of the energetic reasons for the success of cycling receptor system are suggested. Whereas the theoretical optimum efficiency is 50% for the cycling receptor system loading itself, the many energy drains for other transfers, maintenance, and downstream work processes reduce the observed efficiencies of the compound chain of energy transfers much below this.

To gain some evidence of the applicability of the optimum efficiency maximum power output in photosynthetic reception, some test of output may be made with input load fixed and output load varied. For the electrical analog Bilig and Plessner (1949) already showed an optimum efficiency for maximum power output. This has been attempted for the living receivers by replotting some published data for the Hill reaction where isolated chloroplasts can be studied with varying concentrations of oxidized substrates provided as downstream loading. The results are given in Fig. 11 with data replotted from Lumry and Spikes (1957) and from Clendenning and Ehrmantraut (1951). Evidence for a parabolic shaped curve of power and loading is thus provided in further support of the generality of the time's speed regulator principle, in which evolutionary selection of the maximum power loading is implied. Armstrong and Odum (1964) showed the parabola for a blue-green algal mat. Further examples are given by Milsum (1966) for muscle, and Tribus (1961) discussing engineering systems presented the general theorem in a new way.

ENERGY DEFINITION OF STRESS

There are many kinds of stress. Some remove organisms; some divert incoming resources, some damage structure as fast as it is produced, some remove whole systems, some increase disordering rates, etc. All such influences have a common property, that of diverting or draining potential energy flows which would have otherwise have led to useful work or storages. Thus we may provide an operational definition of stress as the drain of calories of potential energy flow. One may measure the stress by the change in energy flow of the system, by the disappearence of a previously existing flow, or even by the acceleration of a repair rate for those systems that can respond to the stress with accelerated energy inflows.

Stress and the Limiting Factor Curve

For the situation in complex systems in which energy reserves may be switched and where the rectangular hyperbola of Fig. 8 describes the response to energy input, a stress serves to subtract from the energy available for useful functions and has the effect of moving backward along the limiting factor curve towards its origin. With enough drain, the energy remaining may approach zero. If one turns the axis around, one sees the frequently observed pattern of the dosage response curve for radiation, drugs, pollutants, poisons, and stresses of many kinds, a downward curving of the survival index, functional index, system works, system masses in support, or system diversity in operation. Thus a generalized concept of stress, limiting factor kinetics, and dosage response turn out to be the same property of energy reception.

Currency and Cycling Receptor Materials

Appropriate to this symposium is the general cycle of minerals between the photosynthetic production processes and the consumption-work process. The entities which are necessary to the process cycle, being reused over and over again including scarce mineral elements such as phosphorus, magnesium, calcium, etc. The reaction between each and light is multiplicative as already indicated for a limiting work gate. In a well established climax (steady state) system, the nutrients and organisms have undergone mutual selection process so that the minerals are cycling in the ratio needed by producers and consumers alike as first established by Redfield for the sea. Simplified compartmental diagrams for a climax steady state system like the rain forest shown in Figs. 3 and 6 can be recompartmentalized as in Fig. 12 so as to emphasize relations to the generalized receptor in Fig. 8.

In one sense all of the work developing and stabilizing structure is a part of the work of removing limiting factors such as minerals. The total amount of this work is the total respiration.

The cycling materials that are necessary to a system's functions by carrying and controlling the energies, but which are not the actual energy responsible for the system's operation are sometimes termed a currency. Dollars are the currency of our social system and move in proportion to energy flow but in opposite direction. Boulding (1962) has compared the mineral cycling of ecosystems to currency, although the minerals go in the same direction as the energy flow. The currency whether it be cycling states of chlorophyll, mineral cycles, or dollars is shown in dashed lines using notation from E. P. Odum (1963). Different degrees of control are provided for the relation of energy and currency in Fig. 12. The general system plan has a receiving system and a consumer-work providing system downstream connected back upstream with a loop of necessary work. Mineral and dollar currency are diagrammed. The price-controlled transactor module is shown first with barter and then with circulating money. In the more complex systems one is grouping together as one symbol chains of symbols energy reserves beyond those necessary to operate the basic maintenance and production modules (#1) go into specialists, diversity, and various second priority adaptations that allow the system as a whole to perform better in competition with other alternative combinations that might be in those same circumstances of inputs and drains. The rain forest climax is one example. In B is the revised steady state in which the disordering flow of radiation is causing a drain of energies into increased repair and replacement functions instead of into the advanced specialists and great diversity. The stress climax is an arrested succession in which species capable of net gains are maintained, but unable to pass the network into more complexity because of the continual drain of parts that would otherwise last longer. There are many examples of such stress climaxes including the wave stressed plankton communities of the open sea, the salinity stressed communities of estuaries, the pollution stressed communities of streams, and the fire stressed coastal regions of the southeastern United States. The correlation of successional species with radiation resistance discussed by Woodwell (1967) is thus explained by the pattern of selection for species with rapid turnover and net replacement rates, a property of succession and arrested-successional climaxes. The correlation of radiation sensitivity with size from virus to man (Kaplan and Moses, 1964) may also be explained, since small units maintain themselves with replacement to a greater extent than large ones.

In C is diagrammed the stress climax produced by harvests of yield in forestry or agriculture, which have the same energy drain effect and involve arrested succession. In the rain forest situation the yields of plantations of fast growing cadam trees (Anthocephalus cadamba) might be cited as the yield climax of growing trees for forestry purposes that replaced the former system of protection and maintenance. Outside work controls and harvesting energies gradually go into specialization and diversity if left without the harvest stress and other controls. In the rain forest system in Puerto Rico the net dry weight of Anthocephalus cadamba at two years age was about 20 $g/m^2/day$ compared to the gross photosynthesis of 32 $g/m^2/day$ in the complex forest. Both hold a basic forest system structure, but the climax achieves more gross through spending its yield on complex specialization and organization. The difference of 12 $g/m^2/day$ measured the energy cost of the diversity as well as its value to the total system's competitive role overall. The conversion to Kcalories was made in Fig. 14A using 4.5 Kcal per gram.

Stress is a regular part of all natural ecological systems, some more than others. Many systems which are regarded as ultimates in complexity possible for the particular climate of inputs, outputs, and stresses would have energies available for further specialization and diversity if the stress were removed. Placing some ecosystems in stable conditions in the laboratory thus may cause them to increase their diversity beyond those observed in nature. Arrested succession can be released to learn what the revealed ultimate climax can be. One is reminded of the phenomenon of neotony (paedogenesis). Stress in ecosystems is paedogenetic making the developmental stage into the adult stage. The stress of overdeveloping any one part may serve to arrest the development of other parts.

Summary

Understanding of systems of nature including the ecological systems studied in this symposium require the identification, diagramming, measurement, and eventually simulation of the many work flows that often are relegated to a catch-all category called respiration. The energy circuit language helps to relate the many flows of potential energy into work by imposing the constraint of the thermodynamic laws of budget limitation and entropy tax. Many well established phenomena in this language turn out to be special cases of a few general patterns. Thus chemostat drains, fish and forest harvests, pollution stress, and gamma radiation are all energy drains. The energy contributions of auxiliary limiting factors become identified as fuels with potential energy contributions to the total budget. The modules of the energy circuit language carry with them the previously established kinetics of cycling receptors and limiting factor hyperbolae, which turn out to be energy multipliers, amplifiers, loading controls, and mechanisms for self designing learning loops at the next level of organization. Food chains, turbulent eddy transformations, and stages in photosynthetic compartmental loading seem to be special cases of the optimum efficiency maximum power principle which predicts logarithmic power spectra in energy transformation chains under Darwinian choice generation and natural loop selection. In grazing control theory the insects of the rain forest emerge as specialized shepherds rather than stress pests. Principles of ecology and economics are generalized in the price-control transactor module. The energy network theories begin to show concrete and quantitative means for comparing successful long stable systems like the rain forest with the wildly unstable new networks of urban man and nature, hopefully to guide us in finding mechanisms in one for stabilizing the other.

Acknowledgment

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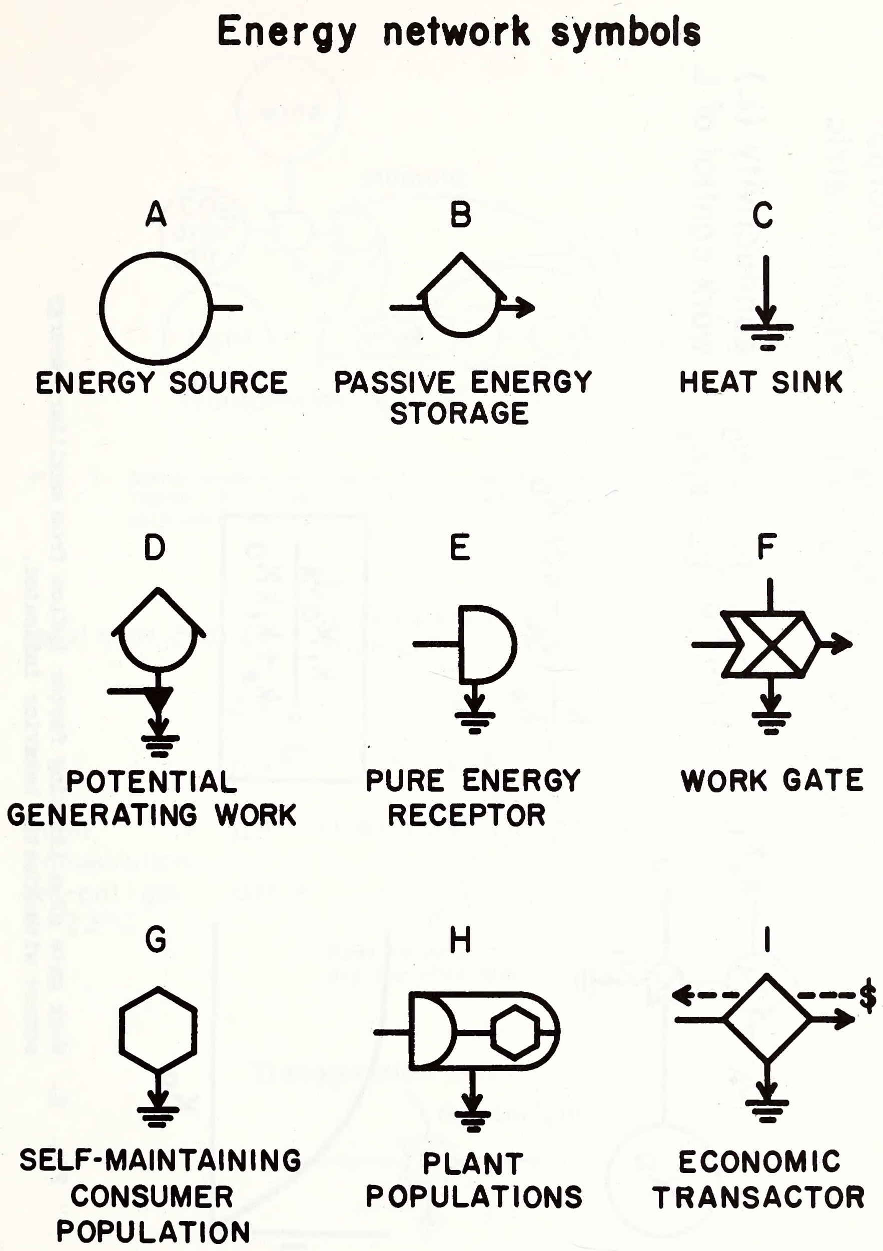
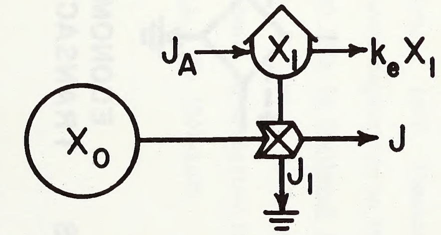


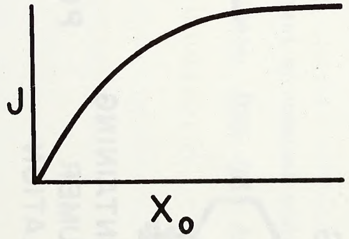
Fig. 1. Modules of the energy circuit language.



$$k_e X_1 = J_A - kJ \begin{cases} k_e X_1 = J_A - J_1 \\ J_1 = kJ \end{cases}$$ input - output stoichometric

$$J = k_1 X_1 X_0 \begin{cases} J = L X_0 \\ L = k_1 X_1 \end{cases}$$ conductivity (L) work control of L

$$J = \frac{k_1}{k_e}(J_A - kJ)\,X_0$$



$$\boxed{J = \frac{k_1 X_0 J_A}{k_e + k_1 k X_0}}$$

Fig. 2. Work gate of a limiting factor inflow from auxiliary energy source with kinetic behavior indicated.

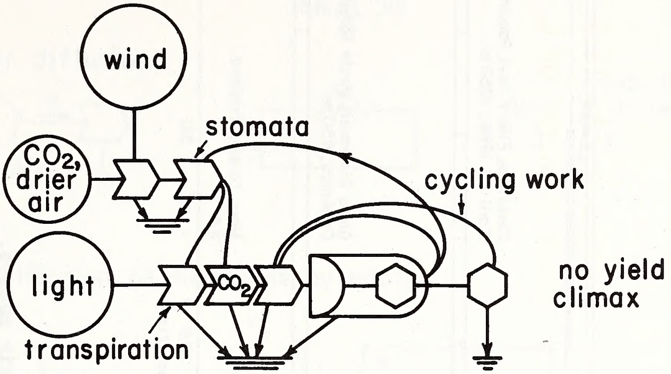


Fig. 3. Energy diagram for some auxiliary fuel flows of the rain forest. A fuel value of inflowing air to the rain forest is calculated below.

$$\text{Total heat change} = \begin{array}{c}\text{Irreversible heat}\\ \text{from potential energy}\end{array} + \begin{array}{c}\text{Reversible}\\ \text{heat changes}\\ \text{of state}\end{array}$$

$$\Delta H = \Delta F + T\Delta S \quad (1)$$

$$\Delta H = RT\ln\frac{p}{p_s} + \text{Latent heat} \quad (2)$$

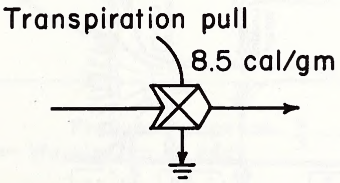
Night transpiration; gm-cal/gm T=22°C

$$\Delta H = (1.987)(295)\left(\ln\frac{20.6}{26.6}\right) + 586 \quad (3)$$

millibars

$$\Delta H = -8.5 + 586 \quad (4)$$

Fuel value of dry air, RH=78%



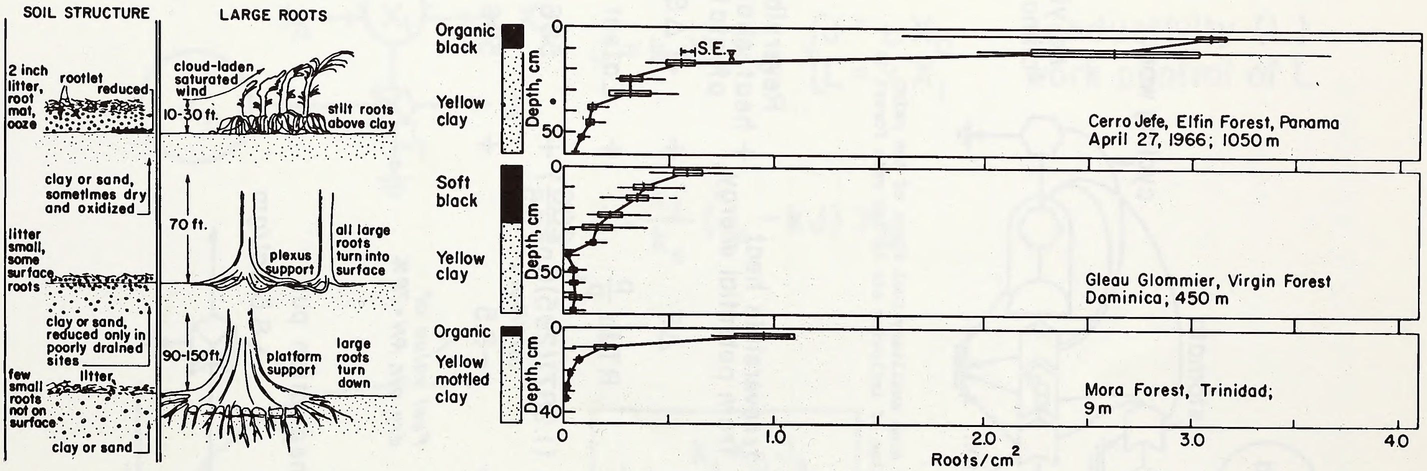


Fig. 4. Forest structure and altitude in moist tropical air masses.

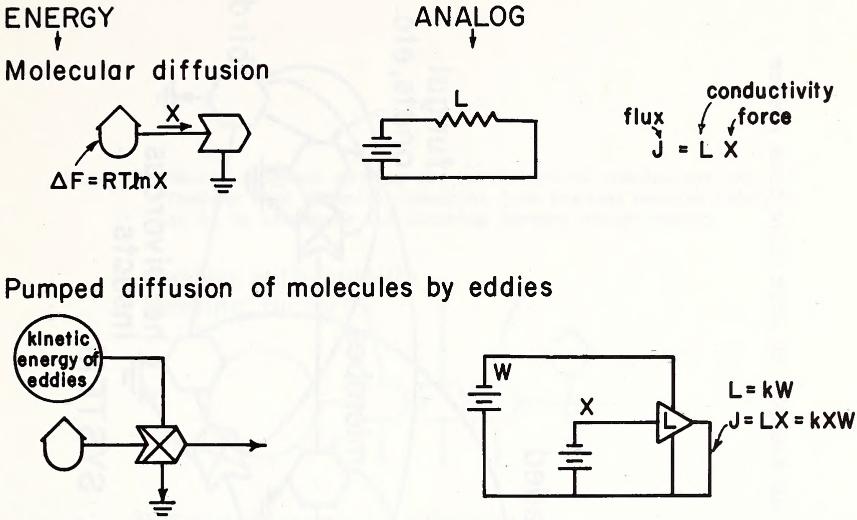
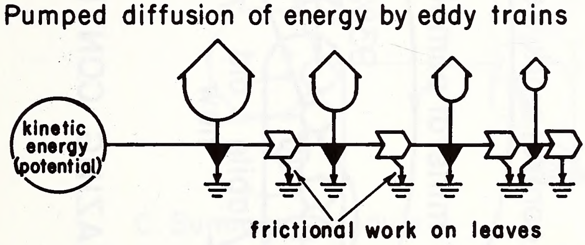


Fig. 5. Energy diagrams for eddy diffusion pumping and chains of eddy transfer.


Pumped diffusion of energy by eddy trains
kinetic energy (potential)
frictional work on leaves

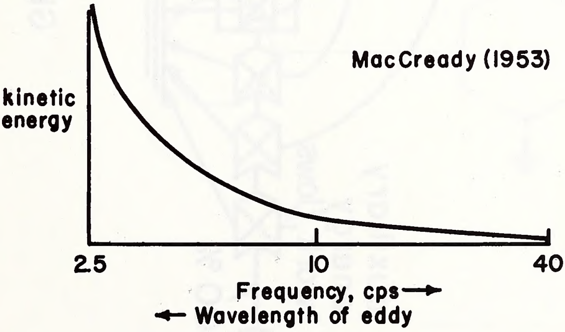


Fig. 6. Grazing control circuit as an example of work flow from system energy pools.

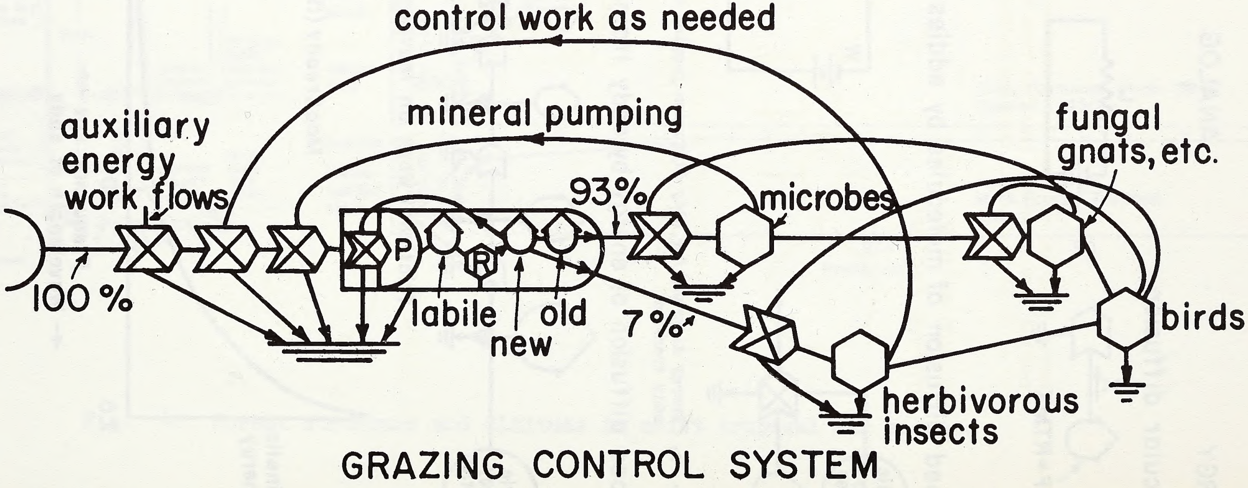
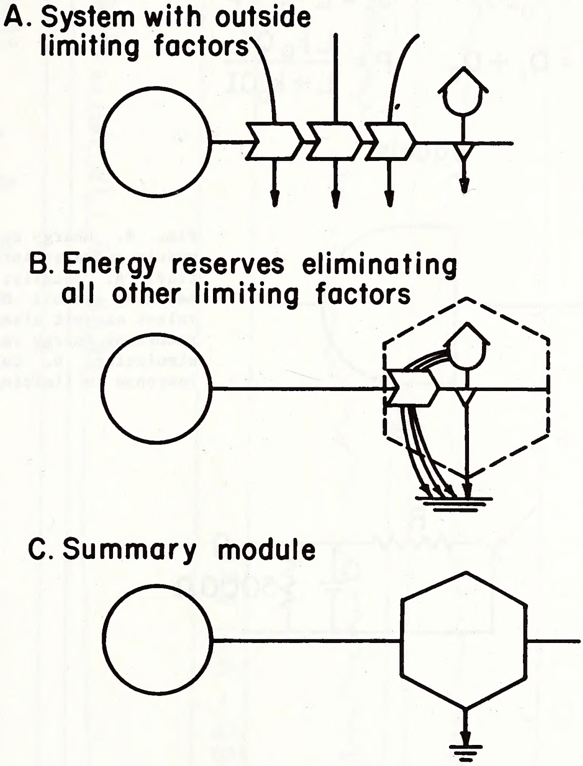


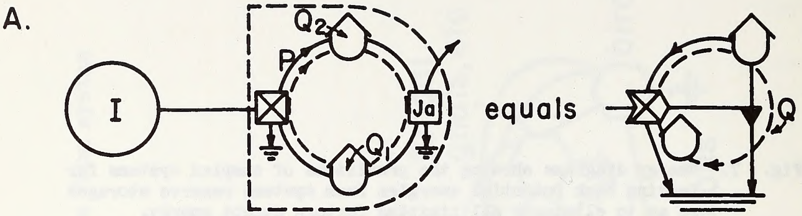
Fig. 7. Energy diagrams showing the provisions of complex systems for feeding back potential energies from systems reserve storages so as to eliminate all limiting factors except energy.



A. System with outside limiting factors

B. Energy reserves eliminating all other limiting factors

C. Summary module



$$P = k_0 I Q_1 \qquad J_a = L\frac{Q_2}{C} = P$$

$$Q = Q_1 + Q_2 \qquad P = \frac{L k_0 Q I}{L + k_0 C I}$$

equals:

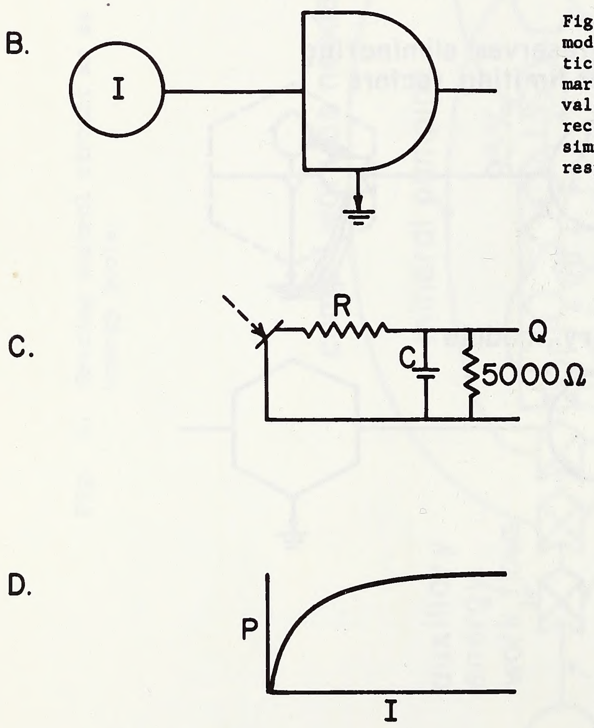


Fig. 8. Energy reception module and associated kinetics. A. Details; B. Summarizing symbol; C. Equivalent circuit also used for recording energy receptor simulation; D. Curve of response to limiting energy.

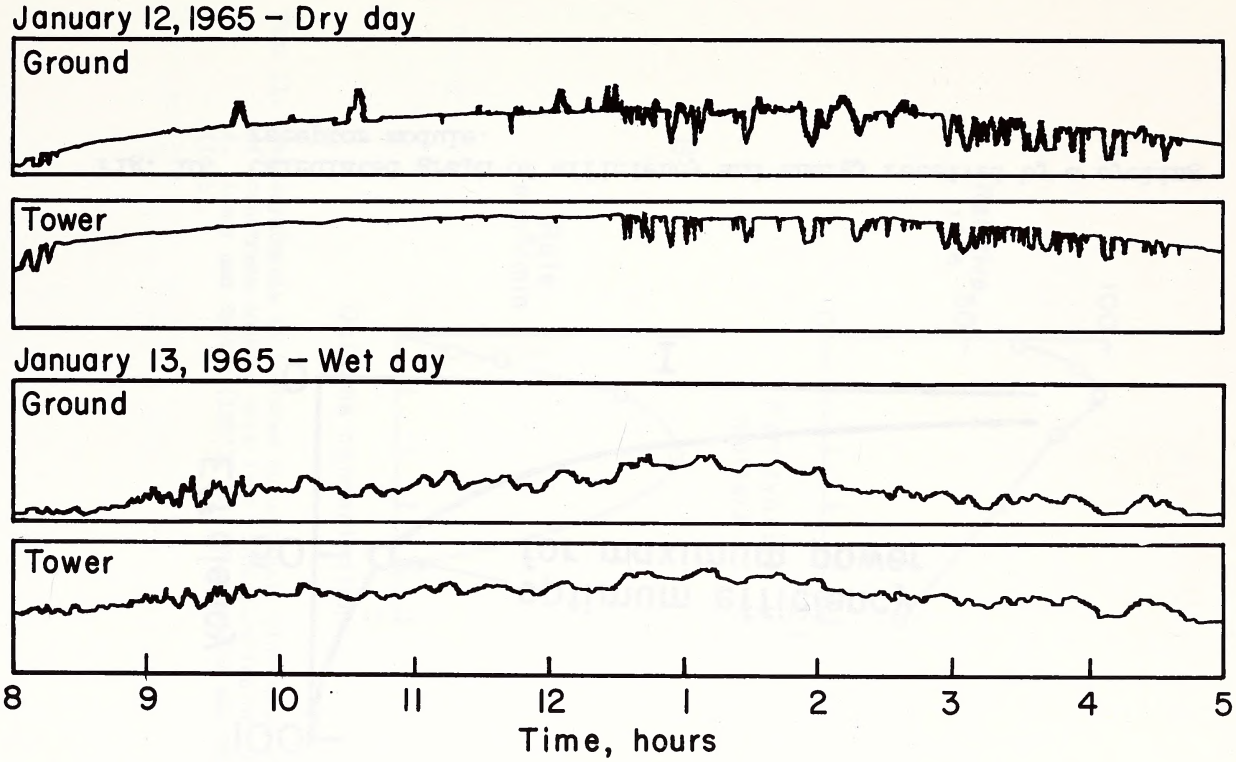


Fig. 9. Hyperbolic output of loaded solar cells used in rain forest as an analog simulator of leaf photosynthesis.

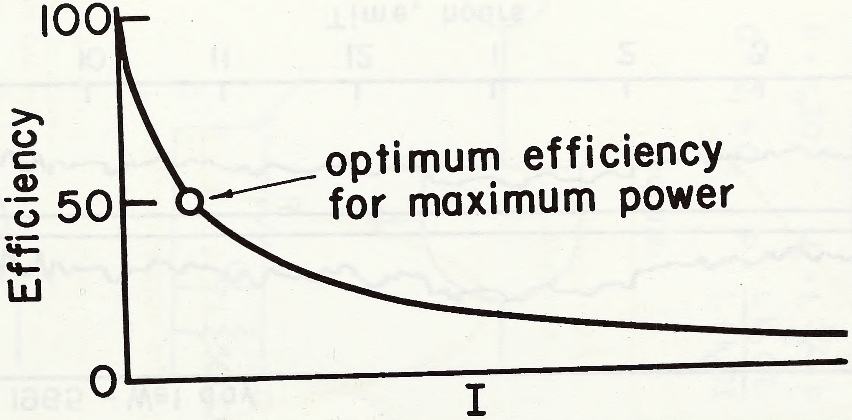


Fig. 10. Calculated graph of efficiency and energy received by a cycling receptor module.

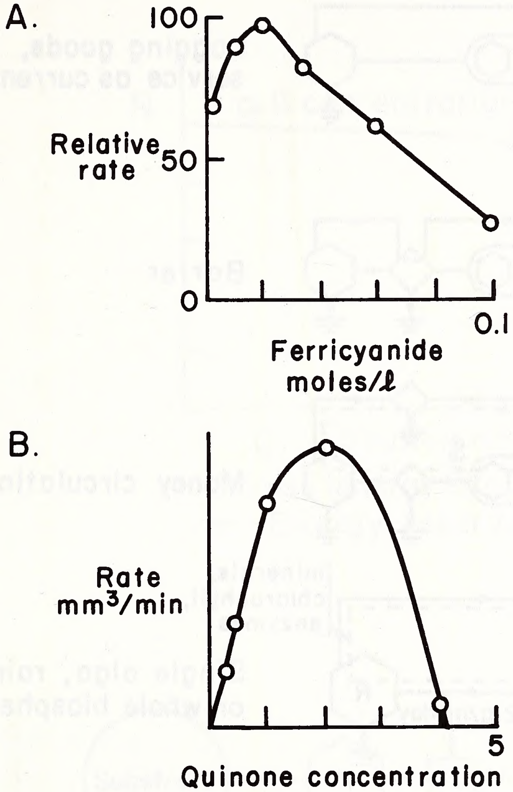


Fig. 11. Photosynthesis in isolated chloroplasts plotted as a function of downstream coupled work load (concentration of oxidants). A. Lumry and Spikes (1957); B. Clendenning and Ehrmantrout (1951).

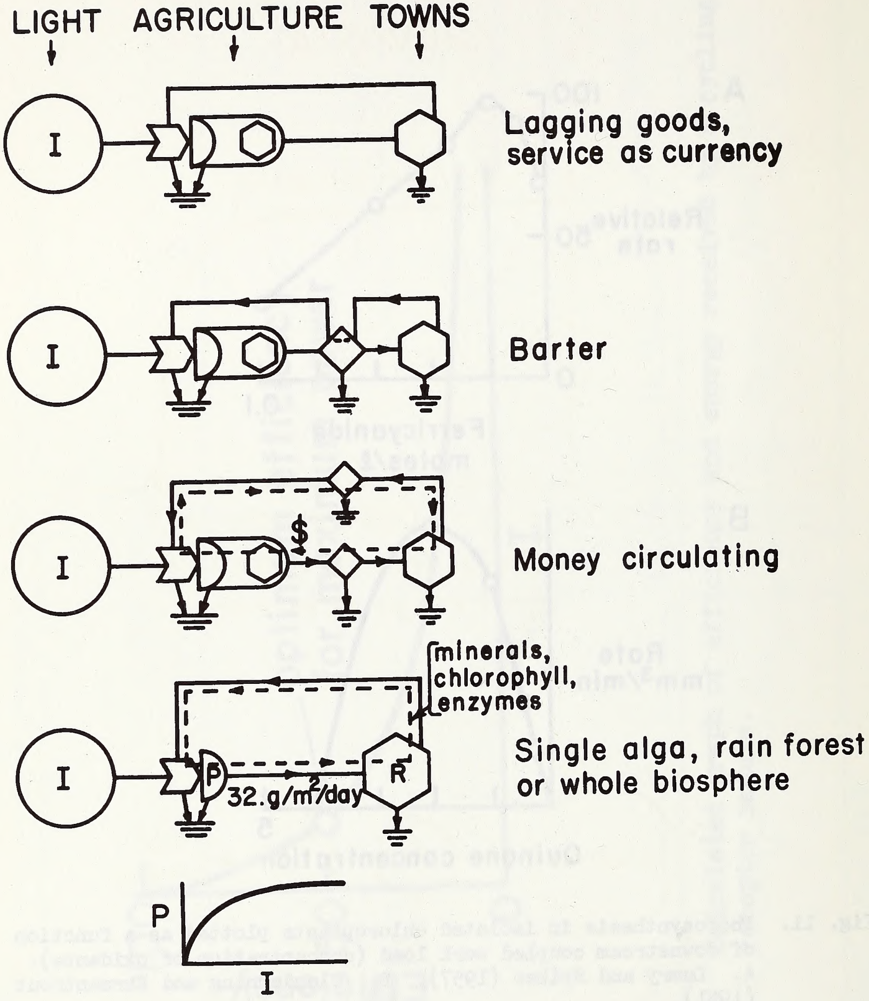

LIGHT
AGRICULTURE
TOWNS
I
Lagging goods, service as currency
I
Barter
I
$
Money circulating
minerals, chlorophyll, enzymes
I
P
R
32.g/m²/day
Single alga, rain forest or whole biosphere
P
I

Fig. 12. Some compound cycling systems arrangements for man and nature, and feedback of work to eliminate all limits except energy.

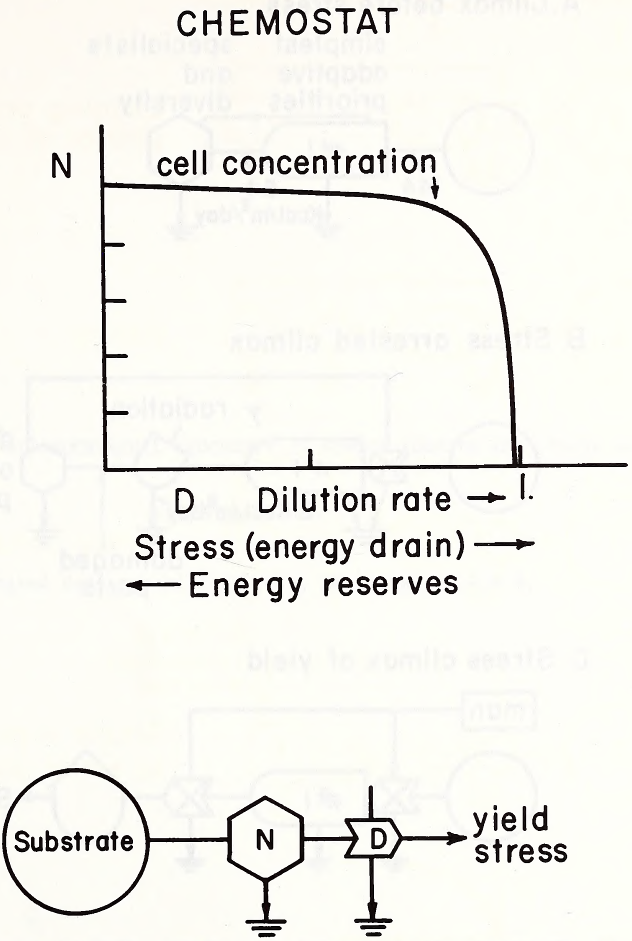


Fig. 13. Chemostats and stress experiments. A. Biomass in a chemostat as a function of wash-out stress as an example of the general stress curve; B. Energy circuit. D is the work flow of the dilution process.

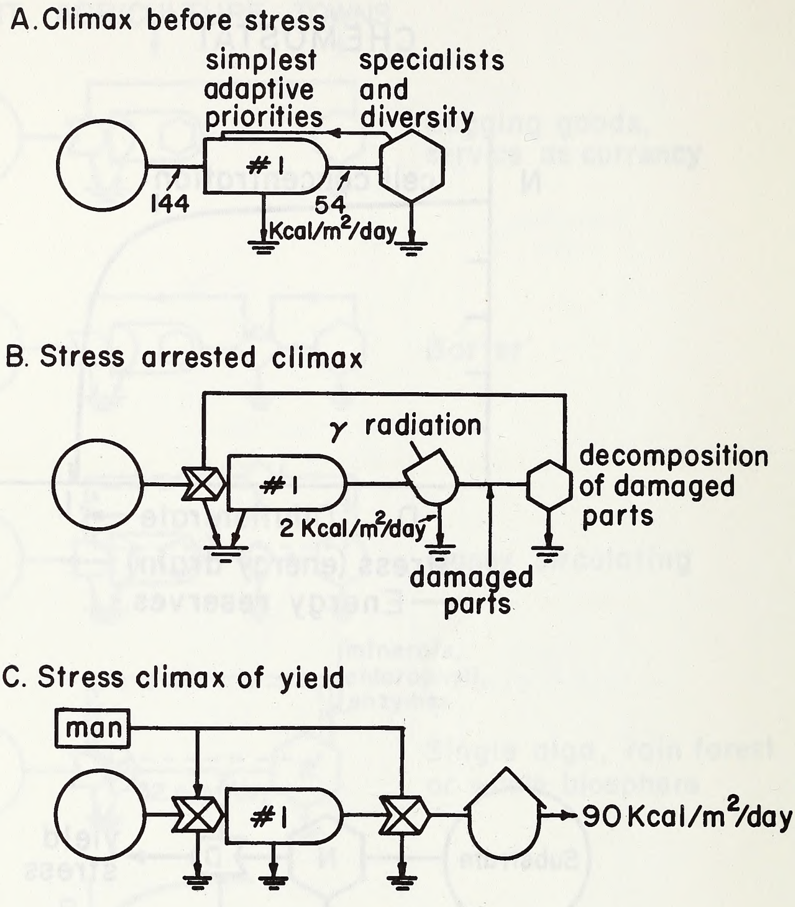

A. Climax before stress
simplest adaptive priorities
specialists and diversity
#1
144
54
Kcal/m²/day
B. Stress arrested climax
γ radiation
#1
2 Kcal/m²/day
decomposition of damaged parts
damaged parts
C. Stress climax of yield
man
#1
90 Kcal/m²/day

Fig. 14. Energy circuits before and after stress. Work of stress drains energies in (B) although some loop feedback stimulus is provided by reuse of the damaged parts in mineralization. Stress by some outside energy control removes yield in (C). These drains divert energy flow that would have provided for additional specialists and diversity before stress as in (A).

PECULIARITIES OF BIOGEOCHEMICAL PROCESSES IN SPRUCE FORESTS AND FILLED AREAS

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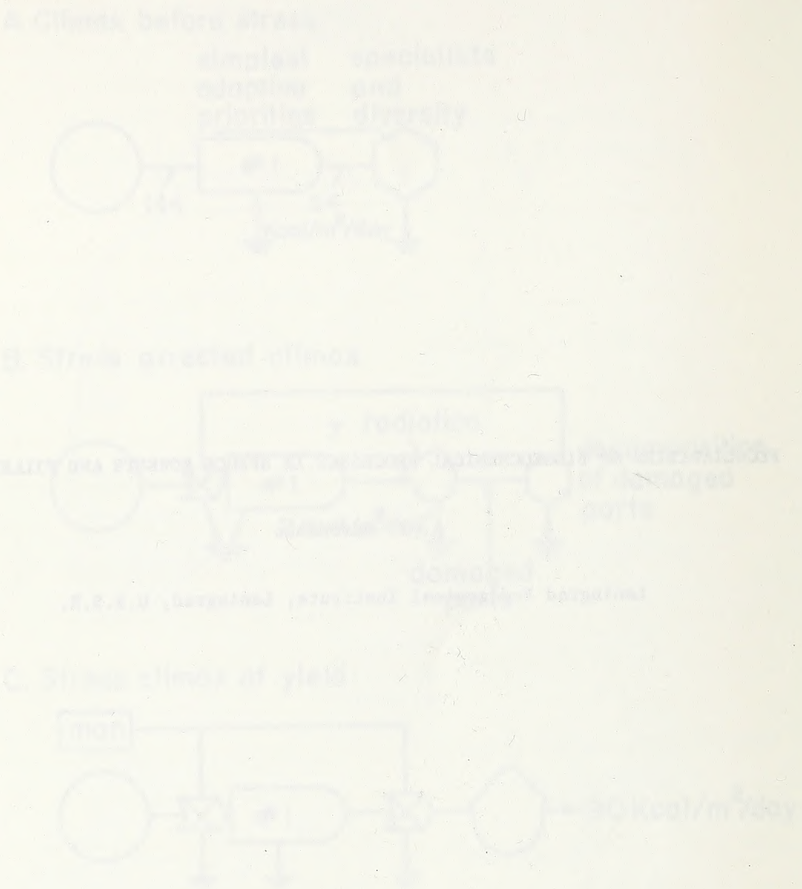
A Climax before stress
simplest
adaptive
priorities
specialists
and
diversity
B Stress arrested climax
radiation
damaged
C Stress climax of yield
man
kcal/m²/day

Fig. 14. [illegible]

Prof. A. I. Marchenko
Leningrad Pedagogical
Institute named after
A. I. Hertsen

PECULIARITIES OF BIOGEOCHEMICAL PROCESSES IN SPRUCE FORESTS AND FILLED AREAS

General Characterization

Spruce forests occupy about 52% of forest area and 65% of the coniferous forests north of the European portion of the USSR. They are the main forest forming kind. Therefore, the investigation of the stories of its biomass, its ash content and the exchange of its cardinal elements in the "soil-plant" system is of considerable practical and theoretical interest.

The investigations carried out by N. P. Remesov, L. N. Bikova, K. M. Smirnova (1959), A. A. Parshevnikov (1962), A. I. Marchenko and E. M. Karlov (1961, 1962), E. I. Rudneva (1964) and many others, in addition to our own investigations carried out with L. A. Varfelomeev, made it possible to find out some regularities in the storage of nitrogen and ash elements in the main types of spruce forests of northern Europe and their return to the forest floor and into the soil.

The results of these investigations can be found in the monograph of L. E. Roden and N. I. Basilevitch (1965). As to the investigation of the dynamics of ground vegetation and of its ash content in the filled areas of spruce forests, this problem has not yet received sufficient attention.

With this aim in view L. A. Varfolomeev and I laid out sample plots of 0.32 hectares both in forests and on filled areas.*)

The first sample plot was laid out in a billberry spruce forest IV class age. Stand composition: 6 S (spruce) 2P (pine) and 2 B (birch). Density of stocking: 1.0. In the living soil cover - billberry (Vaccinium myrtillus h.), green mosses (Polytrichim commyns h. and Hylecomium proliteruns ind.).

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*) Investigations were carried out in 1965-66.

The second plot was laid 400 meters away from the first on a filled area which was 11 years old. In the living soil cover Deschampsia flexuosa Trin., predominated, Vaccinium vitisidaes l, Agrostis Alva), mosses were rare but there were new fillings of birch, aspen and rowan tree. For calculation of ground vegetation the sample areas were divided into plots of one m^2. The most typical of them were chosen and by means of cuts and analysis vegetation composition was investigated with a 4-time replication. On the same plots, soil cuts were made and the number as well as the distribution of roots and dead remnants were calculated in the genetic soil horizons. Samples were taken for physical and chemical analyses.

The calculations show that in a forest based on one m^2 there are 2630 units of moss, and on a filled area only 820, but as to Deschampsia flexuosa Trin. there were 2380 units which almost equals the number of mosses in a forest.*)

Significant changes had taken place in the composition and distribution of roots in the soil (see Table 1).

Small roots in the subsoil and low lying horizons of soils were fully decomposed, whereas big roots (> 20mm) predominating mostly in the A_0 and A_2 horizons are slightly touched by decomposition processes. But the number of these roots is 5 times less whereas the number of small dead roots is 4 times greater in forest soils. It shows that on filled areas about 70% of the vegetation mass has passed the stage of decomposition, humidification and mineralization. Small roots (< 1 mm) belong mostly to Deschampsia flexuosa Trin. and their number is 1.6 times larger than in forest soils. Investigations show that this plant in 2-3 years after clearing out part of a forest accumulates a number of small roots which was calculated as 20-30 centner per hectare. Both in the forest and in the filled areas they die every year, then new ones appear and in the natural conditions of the North, small roots are one of the main sources of enriching the soil with organic substances. The investigations of A. Y. Orlov (1955) show that in a 25-year-old spruce forest the dying but absorbing roots constitute about 50%, and in a 50-year-old forest it is about 20 percent. According to our calculations, in a 80-year-old bill-berry spruce forest small roots form about 8 - 10%, whereas in an 11-year-old area, they form about 40 - 48% of the total store of roots.

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*) Here we name only the predominant plants which play the main role in forming ground soil and an exchange of elements.

Great concentration of small roots of the upper soil horizons of filled areas and more favorable conditions of their mineralization result in the accumulation of organic substances and the fixation in the upper soil horizons of some biogenic elements which are very important for soil formation, root feeding and metabolism. This is reflected in the process of living soil cover formation in the filled area soils. But field investigations show that this process is very unstable and its weakening is connected with the filling of areas with leaf-bearing trees. To show the changes which take place in the soils of filled areas, see the results of physical and chemical analyses (Tables 2 and 3). The analyses show that what is common for the above-mentioned soils is the two member nature of their composition.*) Smaller grained sand and dust accumulation of 40 to 50 cm in thickness covers the deposit of heavier mechanical composition. The sum of particles of physical clay ($<$ 0.01 mm) in lower lying horizons reaches 30%, and in silty ones ($<$ 0.001 mm) - 16-20%, which is 3-5 times higher than in the upper soil horizons.

Such a mechanical composition of soils determines first of all the specific character of the water condition, the penetration of roots in the soil and their distribution along genetic horizons. Investigations show that in the "contact" horizon (A_2/C), there are few small roots, and the large pivoted roots pass by transit into the low-lying horizons, where one can again see the branching off of the roots. This means that the spruce tree belongs to those plants which can easily adapt themselves to different ecological conditions.

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*) We shall not give in this paper the origin of the two member nature of deposits.

The two-member nature of those soils can be found if we analyze their gross chemical composition. In A_2/C horizons we find a small storing of SiO and a relative diminishing of one and a half oxides and other oxides which is the sign of the formation of the second podzol horizon. Its degree of expression depends mainly on the water conditions of those soils. In the upper soil horizon of the filled area (A_0/A_1) the content of calium, phosphorus has increased and the content of H and Al has decreased. The reaction of soil solution (Ph - 4.75, in the filled area - 5.25 has changed favorably. Accumulation and stabilization in the upper soil horizon of the filled area of certain elements is the result of biological accumulation and the sign of the turf process of soil formation, but as has already been mentioned, this process is weakly developed and does not influence the podzol formation.

Gross chemical analysis clearly shows that the disintegration of the mineral portion puts the products of disintegration into the lower horizons and that there is a relative accumulation of SiO in the A_2 horizon. In other genetic soil horizons with the exception of the contact one, the distribution of oxides takes place rather regularly and their quantitative content is rather high which is a sign of the weak weathering of primary elements.

The humus in forests soils and filled areas is rather mobile and can penetrate to the entire depth of the soil profile with a small shortage in the B horizon. Past investigations show that in the early years on filled areas one can see more intensive disintegration of the forest covering, an increase in the solubility of humus, the content of fulva-oxides and the increase in the relation of C:N, while the expanded washing out region and the enriching of the soil with oxide solutions acts favorably on the process of podzol formation in the early years of filled areas.

The appearance of herbaceous vegetation on filled areas results in biological accumulation and the stabilization of primary elements, in some changes in the humus composition and in the appearance of turf process. But this process is interrupted by the natural process of forest growth and by the formation of a compact mass of small-leaf trees. This in its turn leads to the decrease of cereal grasses and to the increase of the influence of green mosses which result in the weakening of turf formation.

The content of certain elements in the vegetative cover of the filled area differs considerably. Thus, in the middle layer ($A_0 2$) the accumulative activity of small roots can be seen, as well as that of tillering knots and the roots of Deschampsia flexuosa Trin. Here we can find a higher ash content, and in it Ca, Mg, K, P. These data do not coincide with those of other investigators (Tatarinov 1957), who maintain that these elements predominate in the third layer ($A_0 3$). Considering these analyses on the whole, we can say that according to its ecological properties Deschampsia flexuosa Trin. cannot influence considerably, the accumulation and exchange of elements, nor can it change the progress of biological transformations in the soil. This plant still accounts for stabilization in the vegetation cover of that portion of the ash elements which is freed through mineralization, as well as for the amorphous Si oxide which is formed in the fallen leaves and disintegration.

The Mineral Content of the Ground Vegetation in a Billberry-Spruce Forest and on its Filled Area

II

In order to find out the content of the ground vegetation and the cover, chemical analyses of the ash content were carried out. The results can be seen on Table 4. From this table one can see that both the vegetation and the cover of the filled area differ from those of a forest in the higher content of ash, nitrogen, and of some mineral elements.

The ground vegetation of the filled area contains: ash - 481.3 kg/hectare, ash chemical elements - 263.7 kg/hectare, while in a forest ash - 343.0 and chemical elements - 181.2 kg/hectare. At the same time, the ground vegetation and separate layers of the soil of the filled area have an ash content which is 2-3 times higher if compared with those of a forest.

The content of silicon in a forest is 66.9, Ca - 55.4 kg/hectare while in the filled area it is 88.1 and 88.7 kg/hectare. The filled area has more Mg, Mn, K, S and less Fe and Al.

Nitrogen dominates in the live biomass. In the ground vegetation of the billberry-spruce forest it is represented by a quantity which is almost equal to the sum of all chemical elements (28.6-28.10); in the upper layer of the cover ($A_0$1) its content diminishes to (8.5) and in the lower layers its content increases to 53.0% of the sum of chemical elements. In the ground vegetation of the filled area and in the following layers, except the third one (A_0 3), there is more nitrogen and chemical elements than in the forest. The content of nitrogen here is 44.0 - 40.0%. The second group of elements in a filled area are K, Si, Ca, and in a forest they are - Ca, K, Si, P. Besides in a forest there are P, Mg, Fe, Mn, Al, and S, whereas on a filled area - Mn, Mg, Fe, Al and S.

This high ash content and the increase of some chemical elements can be accounted by their storage in the Deschampsia Flexuosa Trin. We find the same data in the earlier investigations made on Kolguev Island by Bogdanovskaya-Ginef (1938). She asserted that this plant has a high ash content which includes over 30% of silica quartz. There are other opinions. A German investigator Höhne (1962) considers Deschampsia Flexuosa Trin. to have a low ash content, with a small amount of Si, Ca, Mg, P and a high content of Mn. The low content of Si in this plant can be explained by a sharp difference in the natural conditions, which results in different biogeochemical processes in the soils and the forest of Northeastern Europe. Our investigations show that in the upper layer of the soil of the filled area ($A_0$1 and $A_0$2) the Si content is 2-3 times higher than in the forest.

The accumulation and stabilization of mineral elements and of N on filled areas and in the forest can be represented as follows:

On a filled area: $$\mathrm{N} > \mathrm{K} > \mathrm{Si} > \mathrm{Ca} \begin{array}{c}\mathrm{P}\\ \mathrm{Mg}\\ \mathrm{Fe}\\ \mathrm{Mn}\end{array} > \begin{array}{c}\mathrm{Al}\\ \mathrm{S}\end{array}$$

In a forest: $$\mathrm{N} > \mathrm{Ca} > \mathrm{K} > \mathrm{Si} \begin{array}{c}\mathrm{P}\\ \mathrm{Mn}\\ \mathrm{Mg}\\ \mathrm{Fe}\end{array} > \begin{array}{c}\mathrm{Al}\\ \mathrm{S}\end{array}$$

By absorbtion and fixation of Si Deschampsia Flexuosa Trin. occupies third place in a filled area and fourth in a forest. In a forest after N, Ca takes first place, Mg the sixth, while in a filled area Ca, the fourth, and Mg the eighth place. N both in the forest and in a filled area takes first place.

The results of the analyses showing the absorbtion of chemical elements by plants indicates that the chemical composition of ash in the vegetation of filled areas differs from that of a billberry and spruce forest in the higher content of Si and lesser of Ca, Mg, Fe, Al and S.

As to the relation of strong bases - K, Ca, and Mg and of oxides, Si, S and P, the ash of plants on filled areas is more acid than that of the ground vegetation in a forest. This shows that the biological accumulation of ash elements on filled areas is slower and is accompanied by a considerable storage of Si in the vegetative organs and the forest floor.

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DISTRIBUTION OF ROOTS, DEAD VEGETATION REMNANTS IN THE GENETIC HORIZONS OF SOILS AND THE STORES OF GROUND-VEGETATIONS MASS IN T/HECT.

TABLE I

Genetic horizon and its depth in cm.	Roots & their diameter in cm.	Forest		Filled area	
		Live roots	Dead roots	Live roots	Dead Roots
	20	11.64	- -	0.42	7.66
	5-20	2.38	- -	1.53	0.55
Ao	1-5	1.94	- -	0.96	- -
0-3	1	1.06	- -	1.79	- -
Total		17.02	1.46	4.70	8.21
	20	7.49	- -	0.03	2.34
	5-20	4.58	- -	0.39	1.42
A	1.5	2.45	- -	0.36	0.86
3-10	1	1.16	- -	1.41	- -
Total		15.63	2.41	2.19	4.69
	20	2.61	- -	0.01	1.05
	5-20	2.03	- -	0.28	0.89
B	1-5	1.72	- -	0.44	1.22
11-27	1	0.85	- -	1.63	- -
Total		7.21	1.35	2.36	3.16
	20	0.43	- -	- -	0.46
	5-20	0.76	- -	- -	0.34
B1	1-5	0.66	- -	1.11	0.43
28.40	1	0.24	- -	0.51	- -
Total		2.09	0.41	0.62	1.23
	20	0.14	- -	- -	0.23
	5-20	0.36	- -	- -	0.12
A_2/C	1.5	0.43	- -	0.02	0.15
41-50	1	0.14	- -	0.24	- -
Total		1.07	0.07	0.26	0.50
	20	0.02		- -	0.06
	5-20	0.37		- -	0.30
C1	1-5	0.70		0.01	0.05
70-80	1	0.19		0.13	- -
Total		1.28	0.04	0.40	0.91
Grand Total		44.30	5.74	11.81	18.96

	Forest		Filled area	
	Live cover	Dead Remnants	Live cover	Dead Remnants
Green mosses	1.34	- -	0.76	- -
Berry semi-shrub	0.48	- -	0.48	- -
Deschampsia Flex.T	- -	- -	0.89	- -
	0.10	- -	0.14	- -
Total	1.92	- -	2.27	- -
A_o - Forest Floor	- -	9.03	- -	8.92
A_o2 - Middle Part	- -	18.89	- -	29.34
A_o3 - Lower Part	- -	31.90	- -	26.20
Total	- -	59.82	- -	64 46
Stumps	30.97	- -	- -	11.28
Grand Total	32.89	59.82	2.27	75.74

Table 2

The General Physics and Chemical Characteristics of Soils in a Forest and on a Filled Area

Nos. of cuts	Definition of horizons	Depth in cm	Humus in %	Exchange bases in kg/equiv.			Exchange of acids in mg/equiv.			pH	Mobile Forms			In mm	
				Ca	Mg	Ca+Mg	H	Al	H+Al	H_2o	K Cl	P_2o_5	K_2o	Sum of particles <0.01	Content of particles <0.001
1.	A_o	0-3	- -	24.80	14.30	39.10	4.90	1.04	5.94	4.75	4.25	36.00	- -	- -	- -
	A_2	3-11	0.41	1.85	0.92	2.77	0.08	1.44	1.52	4.75	3.80	3.20	2.50	14.80	2.60
	B	11-27	0.93	1.90	0.42	2.32	0.02	0.84	0.86	5.43	4.70	12.20	7.10	17.70	5.60
	B_1	27-40	0.45	1.77	0.59	2.36	0.03	0.81	0.84	5.80	4.60	9.60	7.10	24.40	9.40
	A_2/C	40-50	0.34	3.18	1.97	5.15	0.04	0.77	0.81	5.15	4.35	13.20	3.20	26.30	15.10
	B/C_1	70-80	- -	5.10	3.54	8.64	- -	- -	- -	7.35	6.40	11.00	10.10	30.50	20.60
2.	A_o/A	2-5	- -	45.80	11.10	56.90	2.76	0.37	3.13	5.25	4.65	39.00	- -	- -	- -
	A_2	5-10	0.35	1.45	0.44	1.89	0.07	0.72	0.79	5.00	3.85	1.50	4.50	14.60	3.30
	B	15-20	1.89	2.06	0.79	2.85	0.05	1.87	1.92	4.95	4.35	6.10	10.40	13.00	1.90
	B_1	25-35	0.33	1.90	1.17	3.07	0.02	1.26	1.28	5.30	4.45	7.00	13.70	4.70	3.20
	A_2/C	40-55	0.26	2.51	1.33	3.84	0.03	1.86	1.89	5.20	4.25	5.10	11.60	13.60	4.00
	B/C_1	70-80	- -	5.03	2.06	7.09	0.03	2.02	2.05	5.20	4.30	13.20	13.80	29.50	16.60

Table 3

GROSS CHEMICAL CONTENT

Nos. of cuts	Horizons	Depth in cm	SiO_2	Al_2O_3	Fe_2O_3	TiO_2	P_2O_5	MnO	CaO	MgO	SO_3	K_2O	Na_2O	$\frac{SiO_2}{R_2O_3}$
	A_o	0-3	69.32	9.83	0.23	0.62	0.82	0.40	3.66	11.13	0.62	0.59	1.53	11.80
	A_2	3-11	85.18	8.30	1.17	0.28	0.06		1.26	0.58	0.18	1.55	1.76	16.00
	B	11-27	78.96	10.44	3.22	0.47	0.14	0.05	1.60	2.10	0.04	1.68	1.89	10.70
1.	B_1	27-40	78.22	11.55	3.87	0.45	0.04	0.05	1.34	1.24	0.12	1.83	1.90	9.50
	A_2/C	40-50	79.15	11.22	3.65	0.61	0.09	0.03	1.32	1.21	0.10	1.92	1.60	9.90
	BC_1	70-80	77.68	10.75	4.26	0.39	0.10	0.05	1.56	1.58	0.06	2.15	1.92	9.80
	A_o/A_1	2-5	67.97	4.19	3.63	0.00	2.40	1.45	10.78	3.58	3.02	2.62	1.84	17.80
	A_2	5-10	85.96	7.38	1.18	0.41	0.02	0.02	1.04	0.59	0.06	1.42	1.53	17.90
2.	B	15-20	77.98	11.60	4.35	0.51	0.08	0.06	1.34	1.09	0.54	1.73	1.46	9.20
	B_1	25-35	79.46	10.82	3.30	0.46	0.06	0.06	1.23	1.51	0.17	1.93	1.50	10.30
	A_2/C	40-55	79.60	10.51	3.41	0.54	0.02	0.05	1.02	1.47	0.15	2.01	1.45	10.60
	B/C_1	70-80	78.16	11.39	4.06	0.46	0.04	0.06	1.14	1.54	0.16	2.13	1.50	9.50

Table 4

MINERAL COMPOSITION OF GROUND VEGETATION IN A SPRUCE FOREST AND ON A FILLED AREA IN % OF DRY SBUSTANCE

Kind of Vegetation	"Pure" ash	Si	Fe	Al	P	Ca	Mg	Mn	K	S	Total N	Sum without N
Ground vegetation in a spruce and billberry forest	3.27	0.22	0.07	0.05	0.16	0.61	0.11	0.13	0.01	0.04	1.50	1.99
Forest litter: A_o	3.43	0.33	0.09	0.03	0.12	0.89	0.13	0.15	0.20	0.03	0.94	1.97
middle part A_o2	3.71	0.68	0.10	0.08	0.11	0.51	0.16	0.04	0.22	0.03	1.25	1.93
lower part A_o3	5.62	1.45	0.25	0.10	0.08	0.56	0.05	0.02	0.28	0.04	1.14	2.79
Ground vegetation of a filled area	5.83	1.07	0.09	0.05	0.19	0.41	0.13	0.08	1.20	0.02	1.46	4.24
upper part - A_o	4.62	0.99	0.03	0.03	0.15	0.61	0.05	0.12	0.36	0.08	1.52	2.48
middle part - A_o2	5.15	0.83	0.07	0.04	0.08	1.07	0.17	0.18	0.27	0.08	1.71	2.79
lower part - A_o3	6.08	1.55	0.15	0.10	0.07	0.77	0.16	0.10	0.20	0.04	1.34	3.14
				In kg/hect. of dry substance								
Ground vegetation in a spruce and billberry forest	62.3	4.3	1.3	0.9	3.1	11.7	2.1	2.5	11.5	0.7	28.6	28.10
upper part - A_o	31.0	3.0	0.8	0.3	1.1	8.2	1.2	1.2	1.8	0.3	8.5	17.90
middle part - A_o2	70.9	12.9	1.9	1.5	2.0	9.8	3.0	0.7	4.2	0.6	23.6	36.60
lower part - A_o3	79.5	46.7	8.4	3.2	2.5	25.7	1.6	0.6	7.4	1.3	36.8	98.60
Ground vegetation of a filled area	130.2	14.3	2.1	1.2	4.3	21.2	3.0	1.8	21.2	0.4	33.2	75.50
upper part - A_o	41.1	8.9	0.8	0.2	1.4	5.6	0.5	1.1	3.3	0.3	13.5	22.10
middle part - A_o2	151.0	24.4	2.0	1.1	2.5	31.2	5.1	5.2	8.1	2.4	50.2	82.00
lower part - A_o3	159.0	40.5	4.1	2.6	2.0	20.7	4.1	2.6	5.8	1.6	35.1	84.00

PRIMARY PRODUCTION AND THE CATION BUDGET OF THE BROOKHAVEN FOREST*

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Most of us will agree that in terrestrial ecosystems the inventory of nutrients retained within the system increases as succession progresses. In the early stages of succession when structure is simple, the inventory is small; in later stages, those approaching climax for instance, the inventory approaches a maximum that is stable, losses equalling inputs, The concept is simple enough to be attractive and appears so closely related to obvious patterns of increasing complexity of structure as not to require verification. The simplicity, however, is a veneer, for the changes in the inventory of nutrients with change in the structure and diversity of the communities include not only total quantities but also relative proportions, pathways of movement, and perhaps even shifts in the nutrients required to sustain primary production. This means that the nutrient budget of an ecosystem is as important a diagnostic criterion as species composition, morphology, production and metabolism, although much less accessible than some of these.

We have measured in considerable detail the primary production, standing crop and net ecosystem production of a late successional oak-pine forest at Brookhaven, Long Island, N. Y. (Woodwell and Whittaker, 1968; Whittaker and Woodwell, 1967, 1968). We have also measured the nutrient inventory and the cycling of nutrients through the primary production. We are restricting our discussion for simplicity in this paper to primary production and the cation budget.

We have used an analytic technique that we have reported previously as "dimension analysis" (Whittaker and Woodwell, 1968). In our application of dimension analysis for this study 15 trees of each species, selected to span the range of sizes in the Long Island forest, were harvested and measured in detail. Regressions were calculated relating attributes that are easily measured, such as basal area or dbh, to complex attributes such as dry weight, weight of bark, branches, or area of leaves. The regressions were used to calculate the standing crop of biomass, net primary production, and related attributes of the community, using phytosociological data from 5 stands selected to include the range of variation in structure of the oak-pine in the region. Data forms and the programs for calculating population and community attributes are available at Brookhaven.

Cations were determined in plant material by atomic absorption spectrophotometry using means of 3-5 samples, each determined separately for each tissue. Precipitation was monitored with 3 rain gauges; percolation with 3 lysimeters buried to a 5 ft. depth.

The standing crop of dry matter in the plant community, excluding humus, is about 10,100 grams/m^2 (101 T/ha). About 75% of the biomass is contributed by the two major oaks: Quercus alba, 32%, and Q. coccinea, 42%. Pinus rigida contributes about 15%; Q. velutina, about 6%. A vaccineaceous shrub layer contains 5% of the biomass. The whole is supported by a net primary production of 1260 grams/m^2 (12 T/ha), about 12% of the standing crop, a high ratio of production to standing crop for temperate forests.

Because the forest is successional, net primary production is partitioned between an annual contribution to the standing crop and support of the communities of heterotrophs. The total contribution to the heterotrophs is estimated as 704 grams/m^2, and this sum is partitioned as indicated in Table 1. Consumption by herbivores, estimated from the area of leaves consumed, is about 32 grams/m^2. There is an annual fall of litter consisting of 264 grams of leaves, 69 grams of branches and bark and 22 grams of fruits. In addition there is a contribution of about 311 grams of roots and 6 grams of herbs to the humus layer (Woodwell and Marples, 1968; Whittaker and Woodwell, 1968).

The energy from net primary production (NPP) stored within the ecosystem adds to the biomass of the plant community. This energy, net ecosystem production (NEP), is the difference between the net primary production and the respiration of the heterotrophs. In a climax community all of the net primary production would be consumed; in this one, there is a net increment of 558 grams added to the total biomass annually.

Knowledge of the net primary production and net ecosystem production, together with an estimate of total respiration of the ecosystem, which was obtained by measurement of CO_2 accumulation during 41 temperature inversions (Woodwell and Dykeman, 1966), makes it possible to solve the production equations for the forest (Table 2). The equation for the ecosystem must be solved first' providing the estimate of gross production, 2662 grams, which can be used to solve the equation for the plant community. The respiration of the plant community is thus 1400 grams, about 53% of gross production and quite in line with other estimates for temperate forests (Westlake, 1963; Whittaker, 1966; Woodwell and Whittaker, 1968).

If we assume that at climax all of the gross production will be channeled into the reppiration of the autotrophs, plus that of the heterotrophs, then the ratio

$$\frac{(Rs_A + Rs_H)}{GP}$$

is an index of succession that ranges between 0 and 1.0. By this criterion the forest is at about 80% of climax.

The NEP, 558 grams/m^2/yr (5.58 T.ha), is partitioned of course among various portions of the ecosystem and it is important to know how it is partitioned to calculate the annual increment of cations added. The partitioning is shown in Table 3: the largest increment, about 28% accruing to the sapwood; 25% to the branches and bark. These increments are, of course, partitioned further among the various species, including the shrubs.

The cations move through these same pathways, but in quantities that are often quite disproportionate to the transfer of dry matter (Table 4). The standing crop contains about 18 grams of K/m^2, 30 grams of Ca, 4 grams of Mg and 0.8 grams of Na, making a total of 53 grams of these cations per m^2. The net primary production contains about 9 grams of cations or 17% of the biomass inventory. You will recall that it contained about 12% of the standing crop of dry matter, meaning that it is on the average richer in cations than the standing crop, a relationship that is hardly surprising since the NPP involves organisms and tissues that are the most actively metabolizing in the ecosystem.

The nutrients contained within the NPP vary greatly when considered as a fraction of the inventory of each cation in the standing crop. They range from 21 and 23% of the standing crop for K and Mg to 13 and 14% for Na and Ca, spanning a factor of nearly 2. NEP, containing 5.8% of the standing crop biomass, also contains 5.8% of the inventory of cations. The variation around this mean among the cations is very small. The range is from 5.2% of the standing crop for K to 6.9% for Mg, meaning only that the ecosystem is accumulating cations in about the same proportions as it holds them at present. This, too, is not especially surprising, but it is interesting to discover how very much richer in nutrients that segment of the NPP that enters the heterotrophs is. The partitioning appears in Figure 1. Thus, while Rs_H accounts for biomass equal to 6.5% of the standing crop, it accounts for cations amounting to more than 11% of the standing crop of cations, including 16% of the K and Mg and about 8% of the Ca and Na. This means simply that roughly 2-3 times as much K and Mg and 1.3 times as much Ca and Na are involved in short-term cycles as are stored in the ecosystem. This, too is a measure of maturity: at present 65% of the cations of NPP flow into the heterotrophs, while about 55% of the dry matter does.

Cations appear to be available in ample quantities to this ecosystem. The sources of cations are of course dust, precipitation, and the erosion of primary minerals. There is an annual increment that is stored as we have shown. Losses are potentially runoff and percolation into the water table. Runoff is almost certainly not an important loss in the Brookhaven forest which is on flat and porous, glacial outwash sands. The principal loss appears to be percolation into the water table. We know its cation content from our collections of the percolate in lysimeters. Total quantities of percolate must be estimated, however, and almost certainly lie within ranges that produce nutrient losses as shown in Table 5.

It is apparent that losses into the water table are either a substantial fraction of or exceed storage. Thus the ecosystem is not now absorbing all of the cations present, despite its successional status.

We can use the nutrient inventory to compare the Brookhaven Forest with others for which similar data can be calculated. First, we have examined a different successional forest on Long Island, the well-known Pinus rigida-Quercus ilicifolia forest that develops after severe and repeated burning (Conard, 1935). We have assumed that the total biomass is the same as in the present forest at Brookhaven, about 10,000 grams/m^2. In such a forest with the biomass split between the pine and the bear oak, total inventory of cations would be about 2/3 that in the present forest (Table 6). K would be about 2/3 that in the more diverse forest; Ca about half, and Mg and Na would exceed that in the present stand. Thus this successional community, common after repetitive, severe burns, with a similar biomass but lower diversity contains not only a lower total inventory of cations but also contains these cations in appreciably different proportions.

The closest comparison available from the literature, which is not rich in comparable data, is Ovington's Stand #6, data from which are summarized in his 1962 review (Ovington, 1962). This was a 55 year old Pinus sylvestris plantation which contained a total inventory of cations of 58.2 grams/m^2, distributed in approximately the same proportions as in the pine-bear oak stand. There was, however, about 3 times as much Na in the Scotch Pine.

The shifts in the inventory of cations and in the proportions in which they are held within the ecosystem reemphasizes that species vary in their nutrient requirements. It would not be at all surprising to discover that species intrinsic to highly developed natural communities have requirements for nutrient elements that are differentiated in much the same ways that phenologies and morphologies have become differentiated, thus adding a further dimension to the concept of "niche" and to the concept of "community".

We have shown in one ecosystem the partitioning of net primary production into its various channels. While the cations follow the same pathways through the ecosystem, they move in quantities that are disproportionate to the quantities of dry matter, a substantially greater fraction of the cations moving through pathways that can properly be assumed to be cyclic than into storage within the system. About 65% of the cations involved in NPP move directly into this cyclic pattern through the heterotroph community. An additional fraction, at present unknown, of that which is stored in the accumulating tissues of the plant community, is probably remobilized by leaching from bark and by translocation from wood and thereby joins the cyclic fraction. Thus the fraction of the total inventory of cations in the ecosystem that is circulating annually is probably slightly in excess of 11%.

When we combine these observations with those discussed earlier, one comes to this picture of the meaning of successional development in terms of nutrient function. Through the course of succession there is increase in the accumulated biomass and an increase in the stock of nutrients held within the system. The mass of leaves and the total nutrients circulated through the leaves may remain approximately stable after the early stages of succession. They must, therefore, become a smaller fraction of the total biomass and the total nutrient inventory. There must be as well an increase in the amount of nutrients circulated through decay of dead wood, barks, and twigs. Thus, as succession progresses the fraction of the inventory recycled increases toward a maximum. While it may not be true that production is greatest at climax, it appears almost certainly true that the potential for sustained use of resources as measured by the cycling of cations becomes greater as the ecosystem approaches climax.

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Table 1. Distribution of net primary production in the Brookhaven Oak-Pine Forest. R_S = respiration; D.A. = dimension analysis (see text for explanation); NEP = Net ecosystem production, the net increase in dry organic matter within one year in the ecosystem; NPP = net primary production; R_{S_H} = respiration of the heterotrophs.

DISTRIBUTION OF NET PRIMARY PRODUCTION

BROOKHAVEN FOREST

	GMS/M^2	Source
I. R_S of Heterotrophs: (R_{S_H}):		
Herbivores (insects)	32	D.A.
Litter:		
Leaves	264	Meas'd
Branches + Bark	69	D.A.
Flowers & Fruits	22	D.A.
Humus:		
Herbs	6	Meas'd
Roots	311	Meas'd
TOTAL	704	

II. Stored in Ecosystem (NEP)

$$NEP = NPP - R_{S_H}$$

$$558 = 1262 - 704$$

Table 2. Production equations, Brookhaven Forest. Numbers in italics were measured; others were calculated from the formulae.

PRODUCTION EQUATIONS--BROOKHAVEN FOREST

Plant Community: $NPP = GP - R_{S_A}$

$$\underline{1262} = 2662 - 1400$$

Ecosystem: $NEP = GP - (R_{S_A} + R_{S_H})$

$$\underline{558} = 2662 - \underline{2104}$$

$$\frac{R_{S_E}}{GP} = \frac{2104}{2662} = \sim 80\% \text{ of Climax}$$

Table 3. The distribution of net ecosystem production (NEP) in the Brookhaven Forest.

DISTRIBUTION OF NET ECOSYSTEM PRODUCTION
BROOKHAVEN FOREST

	GMS/M^2	% Total
Sapwood	154	28
Bark of Stems	28	5
Branches and Bark	137	25
Twigs	62	11
Losses by Leaves Before Absicission	86	15
Total above Ground	467	86
Roots	91	16
Net Ecosystem Production	558 GMS/M^2	

Table 4. The distribution of cations in the net production of the Brookhaven Forest.

NET PRODUCTION-CATIONS

BROOKHAVEN FOREST

	Gm/m^2				
	K	Ca	Mg	Na	Total
Biomass inventory	18.10	30.30	4.36	0.79	53.50
NPP	3.75	4.15	1.01	0.10	9.01
NEP	.95	1.79	0.30	0.05	3.09

Table 5. The cation budget of the Brookhaven Forest.

	CATIONS IN THE BROOKHAVEN FOREST				
			Gm/m^2		
	K	Ca	Mg	Na	Total
Inputs:					
Precipitation and Dust	0.24	0.33	0.21	1.70	2.48
Decay Primary Mineral	1.04-1.17	2.26-2.58	0.71-0.96	0.28-1.06	4.29-5.77
Storage:	0.95	1.79	0.30	0.05	3.09
Losses:					
To Water Table	0.33-0.46	0.80-1.13	0.61-0.86	1.94-2.71	3.68-5.16

Table 6. The inventory of biomass and cations in an early post-fire successional stand and in the present late successional forest at Brookhaven.

BIOMASS INVENTORY-SUCCESSIONAL FOREST

	Dry Matter	K	Ca	Mg	Na	Total
Pinus rigida-Quercus illicifolia						
Biomass inventory	10,192	12.70	16.80	5.49	0.90	35.89
NPP		2.46	2.08	0.75	0.07	5.36
BNL: Quercus-Pinus rigida						
Biomass inventory	10,192	18.07	30.28	4.36	0.79	53.50
NPP		3.75	4.15	1.01	0.10	9.01

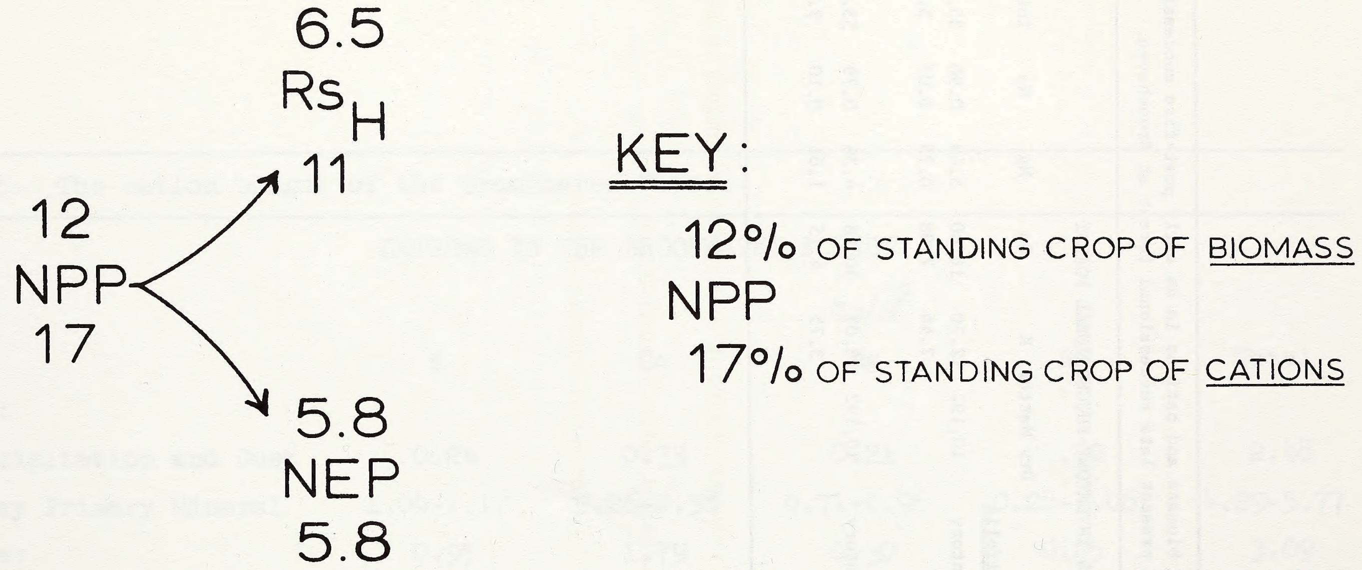
6.5
Rs_H
11
12
NPP
17
5.8
NEP
5.8
KEY:
12% OF STANDING CROP OF BIOMASS
NPP
17% OF STANDING CROP OF CATIONS

Figure 1. The partitioning of net primary production (NPP) and nutrients between heterotroph respiration (Rs_H) and net ecosystem production (NEP).

BIOMASSES, PRODUCTIVITY AND MINERAL CYCLING IN DECIDUOUS MIXED FORESTS IN BELGIUM

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the not confluing crowns have the opportunity of developing at their maximum, without important interference of their neighbors.

As previously said, the coppice is principally formed from hazel and hornbeam; the revolution period is 22 years.

b. When this study was made (1964-67) the oaks were 115-160 years old; they were in the means 24 m high, and their circumference at 1,30 meter varied, for most of them, from 1 to 4 meters.

The average density of the trees was of 110 oaks and 2 ashes (not considered in this study) by hectare, the basal area being 26,3 m2/ha. The coppice formed a continuous layer of Corylus and Carpinus (7-10 meter high and 22 years old (just at the end of a period of revolution). The ground flora was dense (50-80 gs. of dry matter per square meter) and 20-30 cm high.

c. Such a structure, partly due to human action, is very common in Belgium, and has been schematized fig. 3 and 4.

From 1964 to 1967, about 100 trees were felled for exploitation; we used 25 of them for measurement of biomass and productivity; the biomass of the others (standing or felled down) was obtained by extrapolation.

We cut the coppice on five plots of 1 are each. Ground strata was collected on 20 quadrats of 2 or 4 square meters each.

d. The chosen standard surface of 1 ha of forest supported 111 oaks. We did not take into account one big ash and a certain number of regenerating small ones, those trees being protected by the forest's administration.

2. Biomasses

a. Tree strata

The biomass of the trunks (separated in bark, sapwood and heartwood) has been calculated from volume and density; the results (dry weight) are as follows:

Bark	22	t/ha
Sapwood	40,5	t/ha
Heartwood	147,5	t/ha
total	210	t/ha

All the branches and twigs of the 25 fallen trees have been cut up into pieces corresponding to different categories of diameter, which have been weighed fresh on the field; those categories were: 0-1,5 cm diameter; 1,5-3,0; 3,0-5,0; 5,0-7,0 (these four categories constituting the "thin wood"); 7,0-10, 10-15, 15-20, 20-25, >25.(these five categories constituting the "strong wood" or "derbholz"); from each tree, samples of each category of branch pieces were taken and dried in ventilated ovens (85 C), for dry weight estimation; so, the total weight of the crown of each of the 25 fallen trees was obtained; a curve (fig. 2) giving the weight of the crown in function of the diameter of the trunk at 1,30 m height has then been traced, which permitted a good estimation of the weight of the crowns of the remaining 86 trees.

Using this method, the total dry weight of the tree crowns was found to be 84 t/ha; details are given table 1.

The biomass of living leaves has been assimilated to the biomass of fresh fallen leaves (measured on 25 quadrat of one square meter each). The data obtained in this way were 2,7t. leaves by ha. From the category of branches from 0 to 1,5 cm diameter, aged about 10, the current year twigs (with buds) have been separated and weighed; their biomass by hectare, evaluated by extrapolation to the 111 trees, attained 450 kg/ha; this biomass is, of course, annual productivity.

Following a tradition of the Belgion foresters, and from personal measurements, the biomass of the roots has been estimated to 13% of the biomass of the aerial parts, the result was 35,3 t/ha.

b. Coppice strata

On the five plots of 1 are every stem of the coppice has been cut to ground, and cut up into categories of the same sizes as the tree's branches/ Total weight as well as current year twig production, were obtained using the same methods as in #2a.

The results were:

	Bark	Wood	Total
Corylus	1,8	8,6	10,4
Carpinus	2,9	16,0	18,9
Total			29,3 t/ha

The current year twig production was 140 kg for *Corylus* and 190 kg for *Carpinus*. Stumps and roots have been uprooted from trenches of 4 x 1 m, and weighed; the total dry matter of those organs, for *Corylus* and *Carpinus*, was estimated at about 16 t/ha (10 tons of roots, 5,9 tons of stumps).

Leaves biomass has been measured from 25 square meters of litters of freshly fallen leaves; the results were 410 kg *Corylus* leaves and 290 kg *Carpinus* leaves.

c. Ground flora.

The biomass of aerial parts collected on 20 plots of 2 to 4 square meters has been evaluated to 580 kg/ha : after measuring the relation between aerial and subterranean parts of each species, the biomass of subterranean parts has been evaluated to 1100 kg/ha.

d. Total biomass

The total biomass (standing crop) of the deciduous forest of Weve, which is the sum of biomasses given in 2, 2b and 2c, is represented fig. 3; it amounts 380 t/ha. Because of losses in the extraction ofroots, we have majorizated of 10% their estimated biomass.

3. Productivity

For trunks and branches of the felled trees, the productivity of each category has been measured on annual diameter increment related to biomass (10 last years divided by 10). For standing trees, the productivity has been evaluated from the curve fig. 4, which relates the annual productivity of the trunk to its diameter at 1,30 m height.

The sum of the productivity of the trunks and of each category of branches amounts 4,48 t/ha.

For the coppice, the total biomass (including dead wood) has been divided by 20 (approximate age of the populations), which gives 2,2 t/ha.

The biomass of current year shoots, leaves, and ground flora (which is the annual productivity, nearly all aerial organs drying before the end of the year), has been added to these values.

This gives an aerial productivity of 10,8 t/ha.

For underground parts, the evaluation of productivity, as the one of biomass, was empirical and approximative; it must be ameliorated, using time consuming operations. The final result was a total productivity of underground parts of 1 t/ha.

4. Mineral Cycling.

a. Mineral masses and quantities of Nitrogen in the phytocenosis.

Plant organs are not only made of the organic products of photosynthesis and assimilation, but also contain mineral elements; these may be obtained by incineration, and constitute the elements of the "ashes". To be true, those elements have to be deduced from the weighed biomass, if one wants to express the concept of biomass more accurately; nitrogen which enters the organic composition of plants and escapes from the ashes during incineration, must be studied apart of the ashes elements, those forming what may be called the mineralomass. To estimate mineral mass and nitrogen content of the phytocenosis, each part of its leaves, buds, twigs, branches, trunks and roots of all species of all the strata, has been analyzed for the following elements: K, Ca, Mg, P and N; S had to be dropped provisorily, analytical difficulties resulting from its very low content; Si was unimportant in a phytocenosis lacking grasses and sedges.

Fig. 5 gives an example of the complete analysis of an oak in the studied phytocenosis, two oligoelements, Cu and Mn, are given, as well as the considered polyelements.

Table 2 gives another example: the content in minerals of the different species of the ground flora; it shows a high specificity of mineral composition for different species growing on the same soil in the same environment.

The mineral mass and nitrogen quantities by hectare may be calculated from mineral content and biomass of every part of the phytocenosis.

Some details and results are given fig. 6; they may be compared to the total and exchangeable reserve of the soil.

b. Mineral cycling (fig. 7)

The phytocenosis retains the elements taken by the annual productivity of perennial organs (stems, branches, roots); the "retained elements" were thus calculated from annual productivity and mineral contents of these organs.

The phytocenosis returns these elements by litter fall, by rain washing, and by stemflow; we have not considered in the Weve forest the two last events; sc we did not consider the annual importations by rain, but, for general information on those problems, we got results of nearby forests.

Fig. 7 shows the annual mineral cycling based only on the return by littler fall. The absorbed elements are the sum of those which are retained and thos which are returned.

This budget is, in kg/ha

	K	Ca	Mg	N	P
retained	21	42	5	44	4
returned	45	52	9	55	4
absorbed	66	94	14	99	8

281 kg/ha

T/ It shows that the annual needs in polynutrients of an enormous forest biomass of 328 ~~kg~~/ha are only a few kilograms, or tens of kilograms; even on a rich soil which could lead to luxury consumption, the well known frugality of forest phytocenosis is demonstrated again.

To be more complete, we may add the results obtained by S. DENAEYER - DE SMET for annual washing in an other deciduous forest (Virelles-Blaimont) of nearly the same type (*Quercus robur*, *Eagus sylvatica* L. and *Carpinus betulus* co-dominants).

In this forest, the mineral composition of rainwater has been studied for the elements K, Ca and Na in the open and under the canopy of each of the co-dominant species. The results for two successive years (1965, total precipitation 1153 mm; 1966, total precipitation 1227 mm) are given in tabl. 3.

The quantities resulting from washing only may be deduced. If we extrapolate those values to the Weve forest, relating the canopy surface covered by the three principal species to their respective litter quantities, and if we assimilate *Corylus* to *Carpinus*, we obtain the following results:

	kg/ha/an		
	K	Ca	Na
Underneath			
Quercus robur	27,0	35,4	22,8
Corylus avellana	2,8	3,0	2,1
Carpinus betulus	1,9	2,0	1,4
Total	31,7	40,4	26,3

This means that washing is important and that the values given fig. 7 for absorbed K and Ca must be majorated of about 50%. As far as stem flow is considered, the first results obtained in the Virelles-Blaimont forest indicate that it brings to the soil only a few percent of what is brought by litter fall and canopy washing.

The forest of Virelles-Blaimont (near Chimay) is now used for a more complete mineral cycling study as a cpntribution to IBP/PT program.

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Table 1: Oak-ash forest at bois de Weve.
Dry weight of the tree crowns, in kg/ha.

(For explanation, see text)

Categories		Dry Weight (kg/ha)			
N	Diameter (cm)	Bark	Sapwood	Heartwood	Total
3	0 - 1,5		5.878		5.878
4	1,5 - 3	1.600	4.098		5.698
5	3 - 5	2.050	5.281		7.331
6	5 - 7	1.900	6.009		7.909
7	7 - 10	2.890	9.139		12.029
8	10 - 15	3.910	4.870	8.257	17.037
9	15 - 20	2.745	4.306	6.340	13.391
10	20 - 25	1.365	1.841	4.173	7.379
11	> 25	1.060	1.630	4.870	7.560
	Total				84.212

Plant species	% dry weight				
	K	Ca	Mg	N	P
Polygonatum multiflorum	3,8	1,4	0,37	3,0	0,21
Arum maculatum	3,6	0,62	0,21	3,9	0,40
Ornithogalum pyrenaïcum	3,5	0,40	0,20	5,3	0,49
Allium ursinum	3,4	0,70	0,17	4,6	0,37
Narcissus pseudonarcissus	2,8	0,36	0,18	4,3	0,30
Pulmonaria angustifolia	6,6	2,4	0,17	2,2	0,17
Ficaria ranunculoïdes	6,6	1,9	0,20	2,1	0,40
Lamium galeobdolon	5,9	1,4	0,36	2,5	0,25
Primula elatior	4,9	0,64	0,30	2,5	0,19
Viola reichenbachiana	4,4	1,1	0,50	2,1	0.28
Geum rivale	3,5	1,5	0,50	3,0	0,20
Anemone nemorosa	3,0	2,2	0,38	2,8	0,18
Circea lutetiana	3,0	2,0	0,50	2,6	0,16
Hedera helix	1,1	1.2	0,24	1,7	0,10
Rosa arvensis : leaflets	1,9	1,8	0,35	1,8	0,13
petioles + stems	1,2	0,9	0,30	0,8	0,10
Rubus sp. : leaflets	1,5	1,1	0,43	2,5	0,15
petioles + stems	1,0	0,60	0,40	1,0	0.10

Table 2

Polynutrients content of the leaves of the principal species of the groundflora, in an oak-ash forest at Bois de Wève, near Rochefort.

delivered by rain

- Table 3 -

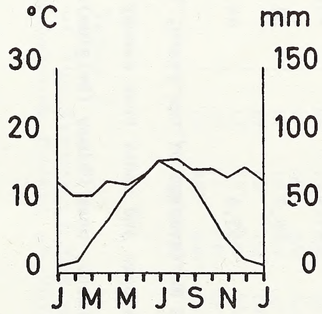
	kg/ha/an			
	K	Ca	Na	
In the open	10,3	16,9	23,5	rain only
Underneath				
Fagus sylvatica	18,3	27,0	23,3	
Carpinus betulus	24,1	25,0	17,3	rain +
Prunus avium	26,7	31,2	24,1	washing
Quercus robur	33,6	44,2	28,3	

Quantities of K, Ca and Na (average of two years, 1965 and 1966) reaching the soil surface in the open and under tree canopy in the mixed oak forest of Virelles-Blaimont, near Chimay (Belgium).

stem-washing not included

Annual t° ± 8°6 Alt. 250 m ± 850 mm Annual rainfall

Vegetation period (days)..... 168
Annual radiation (% Uccle) ...105 summer 103
winter 106
Days of frost 70
Days of winter 6
Days of snow 30
Days of mist 37



Radiation at Uccle (Brussels
85.083 gr.cal/cm^2/year

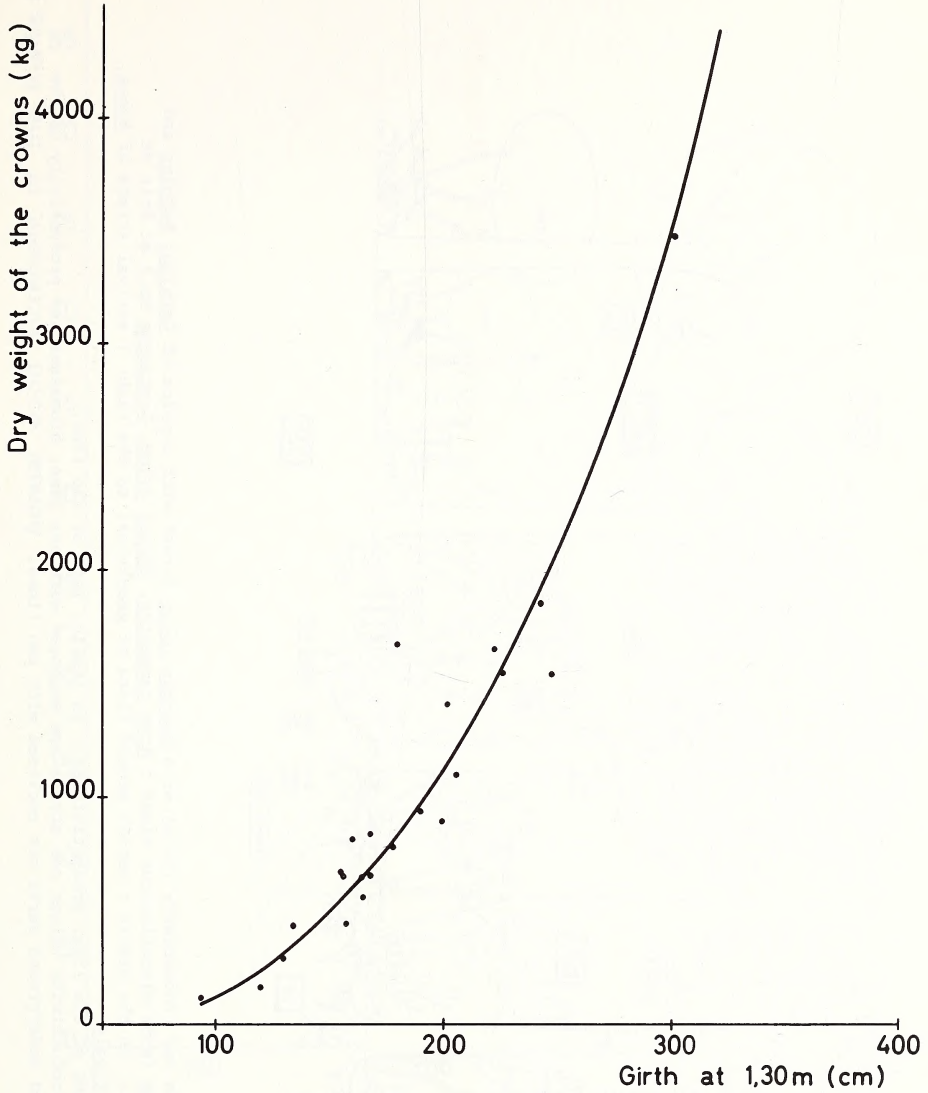


Fig. 2 : Relation between the dry weight of the crowns and the girth of the trunks at 1,3 m hieght, in a population of fullgrown Quercus robur, from 90 to 160 years old, in a forest at Rochefort (Haute Belgique).

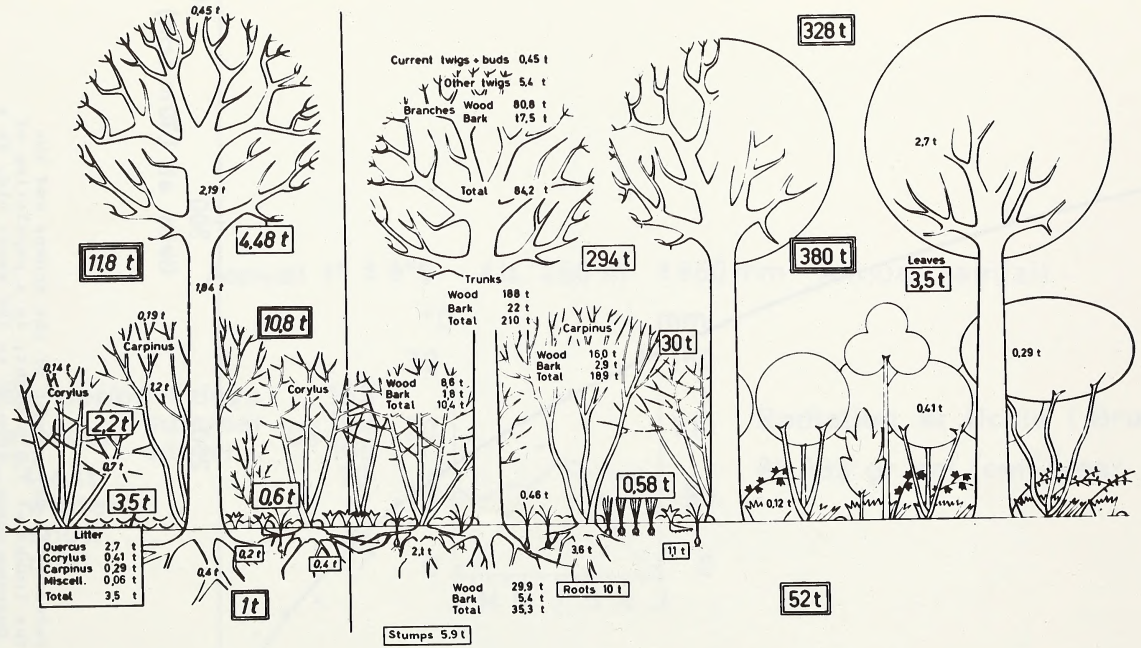


Fig. 3: Biomass and productivity (t/ha) of a Quercus robur forest with coppice of Carpinus betulus and Corylus avellana (some miscellaneous mixed : Acer campestre, Prunus avium, Crataegus sp.) at bois de Weve, Rochefort. In the middle : vernal ground flora of geophytes; to the right : estival strata of Rubus, Rosa, and Geum rivale.

Biomasses : right of the line; productivities : in italic, left of the line.

Biomasses and productivity values per strata are enclosed with one line; biomasses and productivity of the above-ground and underground parts are enclosed with two lines.

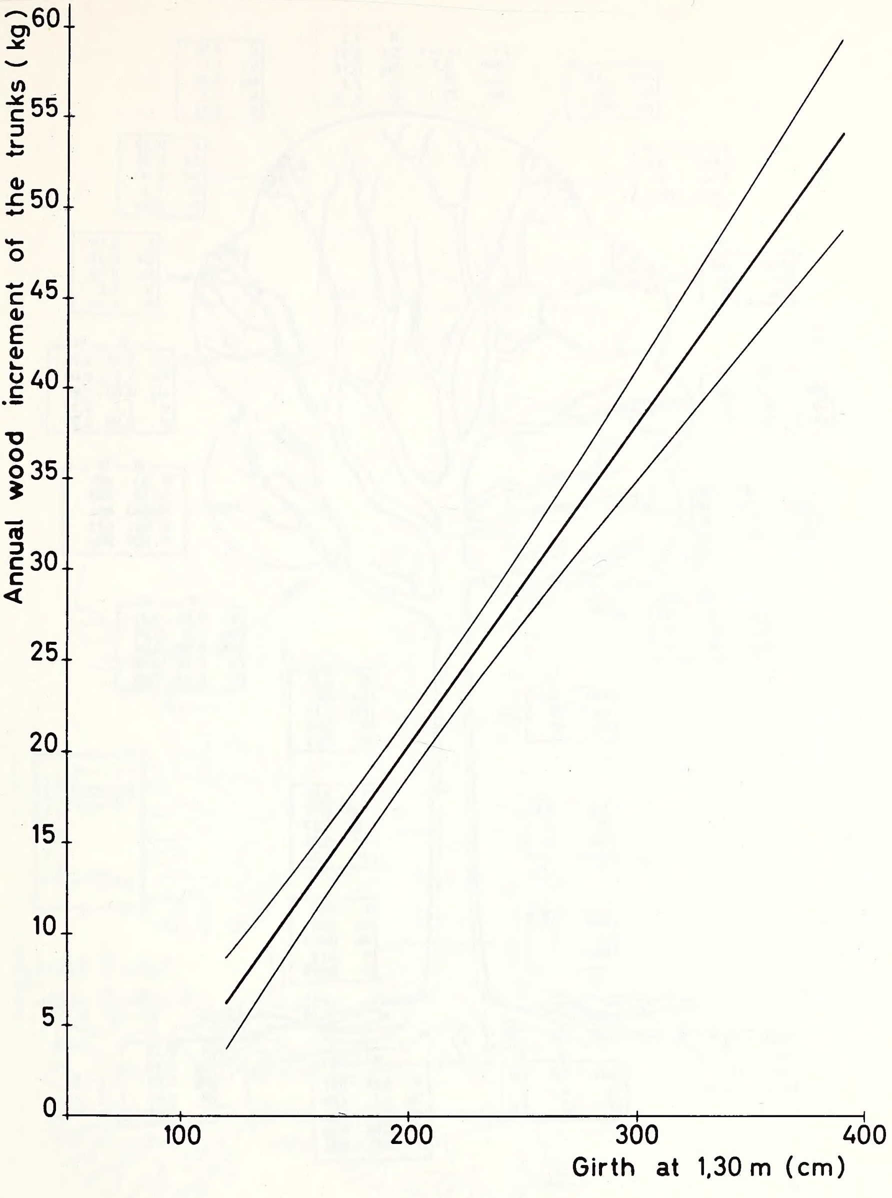


Fig. 4 : Relation between annual wood increment and girth ai 1,3 m hight, in a population of 15 full-grown Quercus robur at bois de Wève, Rochefort (Haute Belgique). Regression line and trust zone calculated with a computer.

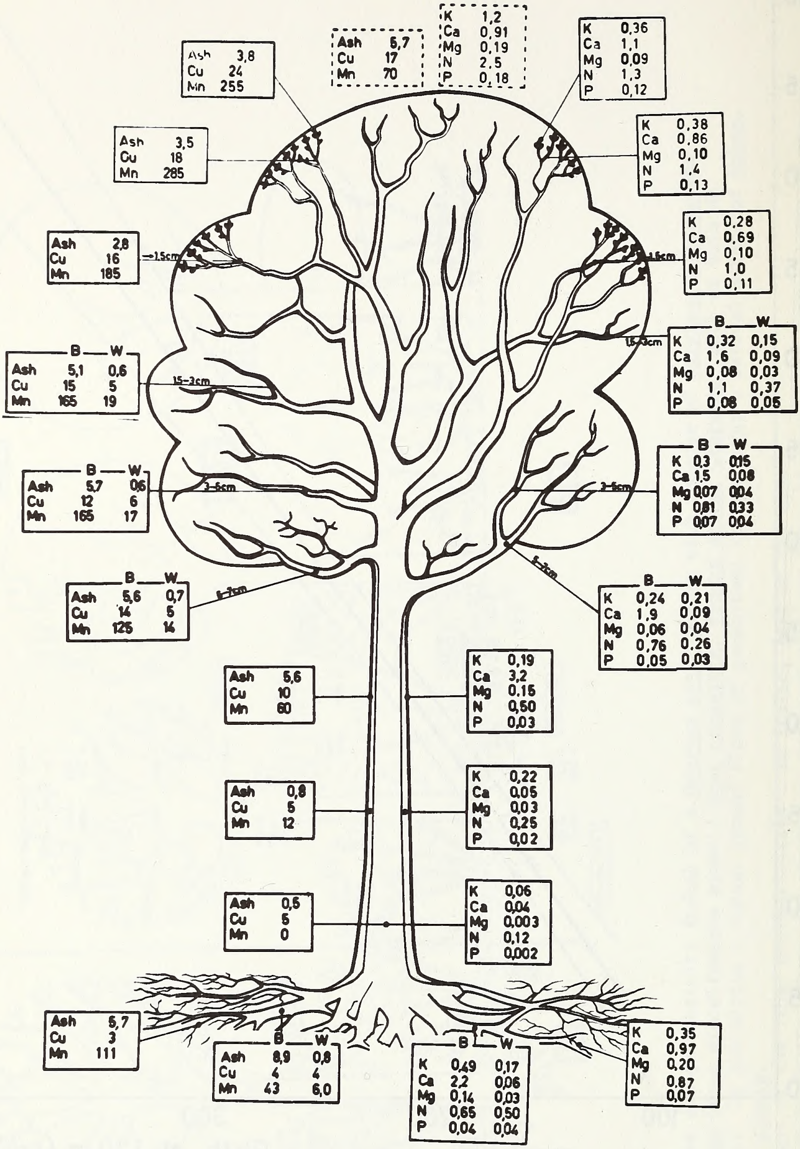


Fig. 5: Ash, polyelements (except S) and some oligoelements content of the different organs from an oak (Quercus robur L.) 147 years old, in the oak-ash forest of Wève (Belgium), 2.4.164.
Right side : K, Ca, Mg, N, P content in % dry matter.
Left side : ash content in % dry matter, Cu and Mn content in ppm.
From top to bottom: dotted framing : content of green leaves (harvested previous year). Continued framing : content of buds, current year twigs, more than one year old twigs but thinner than 1,5 cm diameter; content of bark (B) and wood (W) of branches 1,5 to 3,3 to 5, 5 to 7 cm diameter; content of bark, sapwood and heartwood of the trunk; content of rootlets and bark (B) and wood (W) of roots 3 to 5 cm diameter.

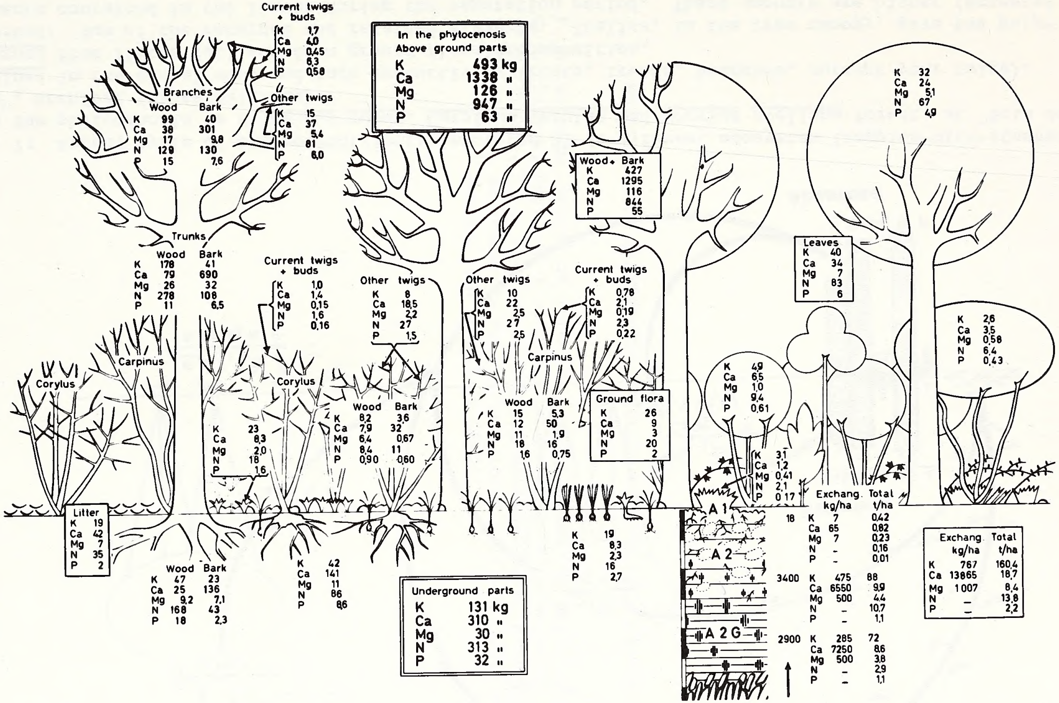


Fig. 6 : Nitrogen and others polynutritients distribution (in kg/ha) in a forest ecosystem (Quercus robur forest with Corylus and Carpinus) at "Bois de Wève", Rochefort (Haute Belgique).

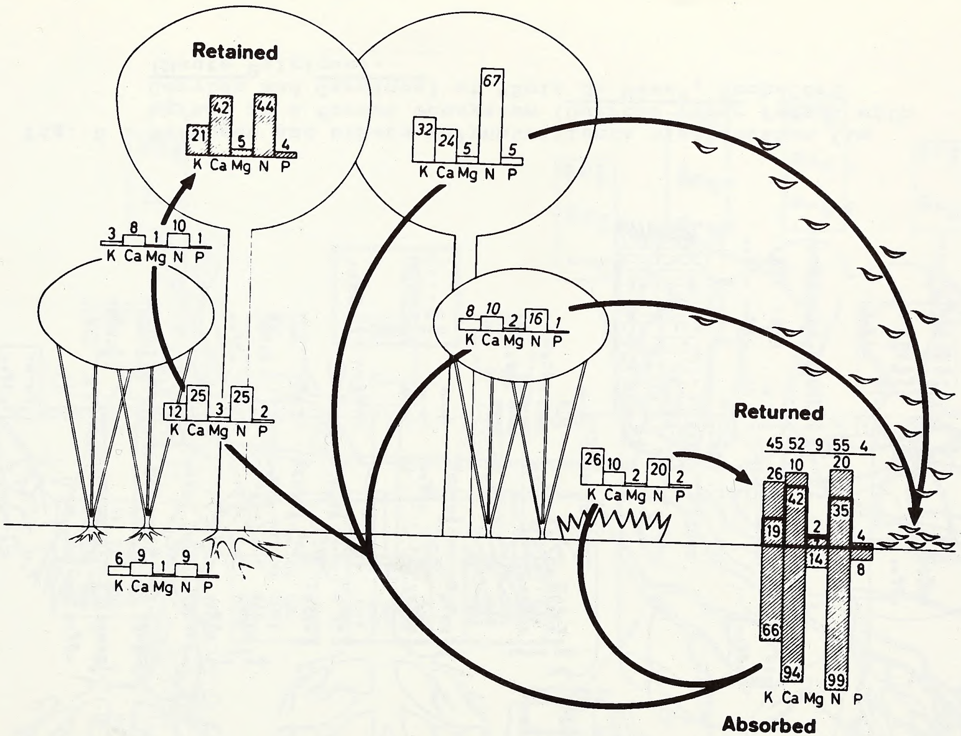


Fig. 7: Annual cycle of the polynutrients (excepted S) in a forest ecosystem (coppice-with-standards) with the phytocenosis is a Quercus robur, Carpinus betulus and Corylus avellana forest, at "Bois de Wève", Rochfort (Haute Belgique).
Retained in the annual wood and bark productivity (roots, trunks, branches, current year twigs).
Returned from litter fall and from ground flora decomposition.
Absorbed: sum of the returned and retained elements. Italics, in the tree canopy, give the poly-elements contained in the leaves during the vegetation period. These amounts are higher (excepted for Ca) than these returned in the litter.

NUTRIENT LOSS ACCELERATED BY CLEAR-CUTTING OF A FOREST ECOSYSTEM

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Nutrient Loss Accelerated by Clear-Cutting of a Forest Ecosystem

Abstract. The forest of a small watershed-ecosystem was cut in order to determine the effects of removal of vegetation on nutrient cycles. Relative to undisturbed ecosystems, the cut ecosystem exhibited accelerated loss of nutrients: nitrogen lost during the first year after cutting was equivalent to the amount annually turned over in an undisturbed system, and losses of cations were 3 to 20 times greater than from comparable undisturbed systems. Possible causes of the pattern of nutrient loss from the cut ecosystem are discussed.

One-third of the land surface of the United States supports forest, and much of it is occasionally harvested. Yet, apart from nutrient losses calculated on the basis of extracted timber products, we have little quantitative data on the effects of harvesting on either the nutrient status of forest ecosystems or the chemistry of stream water draining from them -- which is closely related to the increasingly important problem of eutrophication of stream and river water (1). This paucity of information partly reflects the difficulties of measuring characteristics of massive forest ecosystems, and the fact that nutrient cycles are closely tied to hard-to-measure hydrologic parameters (2).

The input and output of chemicals can be measured and nutrient budgets constructed for forest ecosystems by use of the small-watershed approach (2). For several years we have measured these parameters on six small undisturbed watersheds in the Hubbard Brook Experimental Forest in central New Hampshire (3); here the bedrock is practically impermeable (4), and all liquid water leaves the watersheds by way of first- or second-order streams; the runoff pattern is typical of northern regions having deep snow packs (5). Additional information on topography, geology, climate, and biology is given by

Likens et al. (4).

Chemical relations for these undisturbed forest ecosystems (watersheds) are being established by weekly measurements of dissolved cations and anions entering the ecosystem in all forms of precipitation and leaving the system in stream water. These data, combined with measurements of precipitation and stream flow, enable computation of the input and output of these various elements, as well as annual budgets (2). These results have been reported (4, 6, 7).

In 1965 the forest of one watershed (W-2) was clear-cut in an experiment designed to: (i) determine the effect of clear-cutting on stream flow, (ii) examine some of the fundamental chemical relations of the ecosystem, and (iii) evaluate the effects of forest manipulation on nutrient relations and on eutrophication of stream water. This is a preliminary report of chemical effects observed during the subsequent year.

The experiment began during the winter of 1965-66 when the beech-maple-birch forest (15.6 hectares) was leveled by the U. S. Forest Service. All trees, saplings, and shrubs were cut, dropped in place, and limbed so that no slash was more than 1.5 m above ground. No products were removed from the forest, and great care was taken to minimize erosion of the surface. On 23 June 1966, regrowth of vegetation was inhibited by application of the herbicide Bromacil ($C_9H_{13}BrN_2O_2$) at 28 kg/hectare; approximately 80 percent of the mixture applied was Bromacil; 20 percent was largely inert carrier (8).

Samples of stream water were collected and analyzed weekly, as they had been for 2 years before the cutting; the loss of ions was calculated in terms of kilograms per hectare. Similar measurements on adjacent undisturbed watersheds provided comparative information.

The cutting had a pronounced effect on runoff, which began to increase in May 1966; the cumulative runoff value for 1966 exceeded the expected value by 40 percent. The greatest difference occurred during June through September, when runoff values were 418 percent greater than expected. The difference is directly attributable to the removal of transpiring surface and probably reflects wetter conditions within the soil profile.

The striking loss of nitrate nitrogen in stream water (Fig. 1) suggests that alteration of normal patterns of nitrogen flow played a major role in loss of nutrients from the cutover ecosystem. This loss is best understood by consideration of nitrogen patterns in the undisturbed ecosystem. Runoff data from such systems (7)(Fig. 1) indicate a strong and reproducible seasonal cycle of concentration of nitrate in stream water. High concentrations are associated with the winter period from November through April, while low concentrations persist from April through November.

The decline of nitrate concentrations during May and the low concentrations throughout the summer correlate with heavy nutrient demands by the vegetation and increased heterotrophic activity associated with warming of the soil. The winter concentration pattern of NO_3 -- may be explained in strictly physical terms, since the input of nitrate in precipitation from November through May largely accounts for nitrate lost in stream water during this period. Evaporation from the snow pack may account for some increase in concentration of NO_3 -- in the stream water in the spring. Also, since yearly input of nitrate in precipitation exceeds losses in stream water provide little conclusive evidence of the occurrence of nitrification in these undistrubed acid soils.

Results from the cut watershed demonstrate nitrogen relations of such an ecosystem and indirectly those of the undisturbed ecosystem. Comparison of nitrate concentrations in stream water from watersheds W-6 (undisturbed) and W-2 (cutover) indicates a similar pattern of concentrations throughout 1964 and 1965, prior to cutting, and through May of 1966 (Fig. 1). Beginning on 7 June 1966, 16 days before application of the herbicide, nitrate concentrations in W-2 show a precipitous rise, while the undisturbed ecosystem shows the normal late-spring decline. Allison (9) has documented similar losses of nitrate from uncropped fields or fields carrying poorly established crops. The increase in nitrate concentrations is a clear indication of the occurrence of nitrification in the cutover ecosystem. Since an NH_4^+ substrate is required, the occurrence of nitrification also indicates that soil C:N ratios were favorable for the production of NH_4^+, in excess of heterotrophic needs, sometime before 7 June.

Some of these conclusions must hold for the undisturbed ecosystem; that is to say, sometime prior to 7 June C:N ratios were favorable for the flow of ammonium either to higher plants or to the nitrification process. The low levels of NH_4^+ and NO_3^- in the drainage water of the undisturbed ecosystem (W-6) may attest to the efficiency of the oxidation of NH_4^+ to NO_3^-, and to the efficiency of the vegetation in utilizing NO_3^-. However, Nye and Greenland (10) state that growing, acidifying vegetation represses nitrification; thus the vegetation may draw directly on the NH_4^+ pool, and little nitrate may be produced within the undisturbed ecosystem. In this case, one must assume that cutting drastically altered conditions controlling the nitrification process.

The action of the herbicide in the cutover watershed seems to be one of reinforcing the already well-established trend, of loss of NO_3^-, induced by cutting alone. This action is probably effected through herbicidal destruction of the remaining vegetation -- herbaceous plants and root sprouts. In the event of rapid transformation of all nitrogen in the Bromacil, this source could at best contribute only 5 percent of the nitrogen lost as nitrate.

During 1966 the cutover area showed a net loss of N of 52.8 kg/hectare, compared to a net gain of 4.5 kg/hectare for the undisturbed system (Table 1). If one assumes that the cutover system would have normally gained 4.5 kg/hectare, the adjusted net loss from the cutover system is about 57 kg/hectare. The annual turnover of nitrogen in undisturbed systems is approximately 60 kg/hectare on the basis of an equilibrium system in which annual leaf fall is about 3200 kg/hectare (11) and annual losses of roots are about 800 kg/hectare. Consequently an amount of elemental nitrogen, equivalent to the annual turnover, was lost during the first year following cutting.

Nitrogen losses from W-2 do not take into account volatilization, which accounted for about 12 percent of the total losses from 106 uncropped soils (9). Moreover, denitrification, an anaerobic process, requires a nitrate substrate generated aerobically (12); consequently, for substantial denitrification to occur in fields, aerobic and anaerobic conditions must exist in close proximity. The large increases in cutover watershed suggests that such conditions may have been more common throughout the watershed.

A high level of nitrate ion in the soil solution implies a corresponding concentration of cations and ready leaching (10); precisely this situation prevailed in W-2. Simultaneously with the rise of nitrate, concentrations of Ca^{++}, Mg^{++}, Na^{+}, and K^{+} rose ultimately severalfold. These increases, in combination with the increase in drainage water, led to net losses 9, 8, 3, and 20 times greater, respectively, than similar losses from five undisturbed ecosystems between June 1966 and June 1967. Concentrations of Al^{+++} rose about 1 month later than the initial rise in nitrate, while sulfate showed a sharp drop in concentration, coincident with the rise in nitrate (Fig. 1).

These results indicate that this ecosystem has limited capacity to retain nutrients when the bulk of the vegetation is removed. The accelerated rate of loss of nutrients is related to the cessation of uptake of nutrients by plants and to the larger quantities of drainage water passing through the system. Accelerated losses may also relate to increased mineralization resulting from changes in the physical environment, such as change in temperature or increase in available substrate.

However, the effect of the vegetation on the process of nitrification cannot be overlooked. In the cutover ecosystem the increased loss of cations correlates with the increased loss of nitrate; consequently, if the intact vegetation inhibits the process of nitrification (13) and if removal of the vegetation promotes nitrification, release from inhibition may account for major losses of nutrients from the cutover ecosystem.

These results suggest several conclusions important for environmental management:

1) Clear-cutting tends to deplete the nutrients of a forest ecosystem by (i) reducing transpiration and so increasing the amount of water passing through the system; (ii) simultaneously reducing root surfaces able to remove nutrients from the leaching waters; (iii) removal of nutrients in forest products; (iv) adding to the organic substrate available for immediate mineralization; and (v), in some instances, producing a microclimate more favorable to rapid mineralization. These effects may be important to other types of forest harvesting, depending on the proportion of the forest cut and removed. Loss of nutrients may be greatly accelerated in cutover forests where the soil microbiology leads to an increase of dissolved nitrate in leaching waters (10).

2) Management of forest ecosystems can significantly contribute to eutrophication of stream water. Nitrate concentrations in the small stream from the cutover ecosystem have exceeded established pollution levels (10

parts per million) (14) for more than 1 year, and algal blooms have appeared during the summer.

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15. Supported by NSF grants GB 1144, GB 4169, GB 6757, and GB 6742. We thank Noye Johnson, David Pramer, William Smith, and Garth Voigt for suggestions and for reviewing the manuscript. Contribution 4 of the Hubbard Brook Ecosystem Study; a contribution to the U. S. program for the International Hydrological Decade, and to the International Biological Program.

Table 1. Partial nitrogen budgets for watersheds 6 (13.2 hectares) and 2 (15.6 hectares); all data are in kilograms of elemental nitrogen per hectare. Gains by biological fixation and losses by volatilization are not included. Watershed 2 was cut in the winter of 1965-1966.

Year	Input in precipitation		Output in stream water		Net gains (+) losses (-)	
	NH_4-N	NO_3-N	NH_4-N	NO_3-N	NH_4-N	NO_3-N
			Watershed 6 (undisturbed)			
1965	2.1	2.8	0.6	1.0	+1.5	+1.8
1966	2.0	4.5	0.5	1.5	+1.5	+3.0
			Watershed 2 (cutover)			
1965	2.1	2.8	0.4	1.3	+1.7	+1.5
1966	2.0	4.5	1.2	58.1	+0.8	-53.6

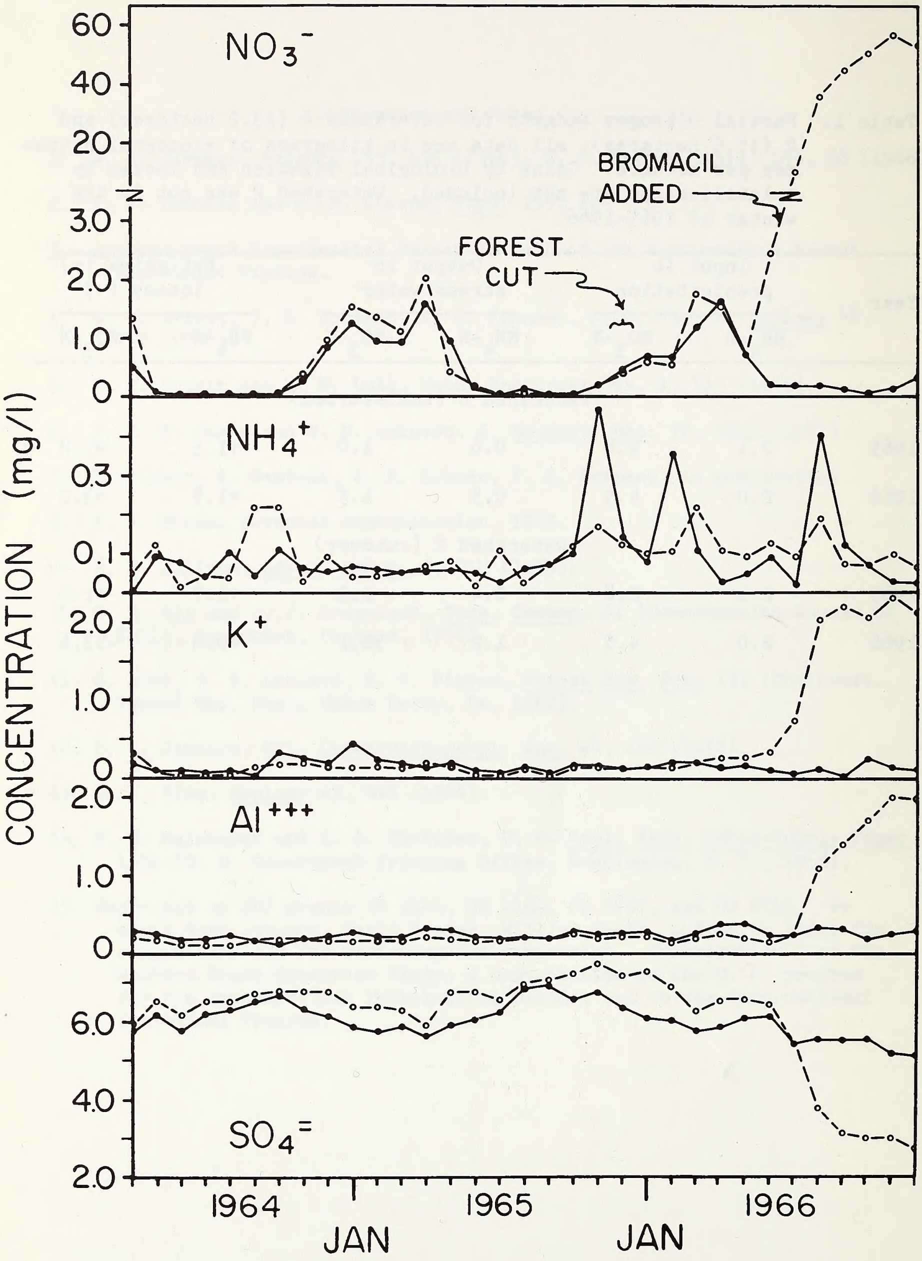

Fig. 1. Average monthly concentrations of selected cations and anions in stream water draining from forest ecosystems undisturbed (solid lines) and clear-cut during the winter of 1965-66 (dashed lines).

DISTRIBUTION AND CYCLING OF NITROGEN, PHOSPHORUS, POTASSIUM, AND CALCIUM IN A SECOND-GROWTH DOUGLAS-FIR ECOSYSTEM

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ABSTRACT

Distribution and Cycling of Nitrogen, Phosphorus, Potassium, and Calcium in a Second-Growth Douglas-Fir Ecosystem[1]

D.W. Cole, S.P. Gessel, and S.F. Dice[2]

The distribution and transfer of elements have been followed in a second-growth Douglas-fir ecosystem at the Cedar River research area in western Washington. The ecosystem consists of a 36-year-old Douglas-fir plantation located on a glacial outwash soil.

Rates of elemental transfer have been measured between the forest and the forest floor, between the forest floor and mineral soil, and through the soil system. Uptake rates of the vegetation, calculated from redistribution and accumulation patterns within the vegetation, are reported. The efficiency of elemental utilization by the vegetation and change in the elemental status of the soil through elemental uptake are discussed.

[1] Contribution from the College of Forest Resources, University of Washington. This investigation was supported in part by grants from the National Science Foundation (BG 1357) and the Public Health Service (5 T01 WP0043: 743-01,2,3).

[2] Assistant Professor of Forest Soils, Professor and Associate Dean, and Research Assistant, respectively.

Distribution and Cycling of Nitrogen, Phosphorus, Potassium, and Calcium in a Second-Growth Douglas-Fir Ecosystem

By

D.W. Cole, S.P. Gessel, and S.F. Dice

INTRODUCTION

Mineral cycling within Douglas-fir ecosystems of the Pacific Northwest has been studied for a number of years. These studies originated in the research on soil fertility and mineral nutrient requirements of the Douglas-fir that was developed at the College of Forest Resources and Botany Department of the University of Washington. (Gessel, Walker, and Haddock, 1951) (Gessel and Walker, 1956). Heilman and Gessel (1963) expanded this initial research by describing the nitrogen regime and behavior of nitrogenous fertilizer within six Douglas-fir ecosystems each respresenting a different age class. Cole, Gessel, and Held (1961) using a tension lysimeter system, reported on the elemental transfer through discrete components of the soil and forest floor. The elemental flux between the forest floor, soil, and vegetative components was further defined with radio tracers of phosphorus, calcium, and rubidium. (Riekerk and Gessel, 1965) (Riekerk, 1967).

The desirability of establishing a field research area specifically to study pathways, rates, and processes of elemental transfer within a forest ecosystem became evident. Therefore, in 1961 an area located on an outwash terrace of the Cedar River was selected. This area was particularly desirable because of the uniformity of both the vegetation and soil components.

A series of treatments was initiated to examine the relationships between components of the ecosystem. These treatments included changing the elemental distribution by adding fertilizers (Cole and Gessel, 1965) and changing the elemental cycle by removing the forest vegetation (Gessel and Cole, 1965).

This article composites information developed at the site regarding mineral cycling in a Douglas-fir ecosystem. The elements nitrogen, phosphorus, potassium, and calcium have been selected to provide a contrast between different types of transfer processes. The distribution, annual uptake and accumulation, and transfer rates of these elements are characterized and interpreted.

The study was conducted at the Cedar River Research Station, an area specifically developed to study elemental cycling in second-growth forest stands (Cole and Gessel, in press). The research area is located on a lower terrace of the Cedar River, approximately 40 miles southeast of the University of Washington campus. This terrace was formed during the recessional stage of the Fraser Glaciation (12,000 B.P.). Coarse, well drained soils, typically an Everett series, have been developed from this outwash material. A chemical, physical, and morphological description of the soil is listed in Table 13 (Appendix).

The original forest was removed between 1910 and 1920. After many wild fires crossed the area, a plantation of Douglas-fir (*Pseudotsuga menziesii*) was established in 1931 at a stocking of 2223 trees/ha. This plantation is now 36 years old; the codominate trees are approximately 18 m high (site index 130) and the basal area is 3.77 m^2/ha. Salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), bracken fern (*Pteridium aguilinum* var. *pubescens*), huckleberry (*Vaccinium parvifolium*), and a scattering of twin flower (*Linnaea borealis* var. *americana*) comprise the principal understory species.

In scattered area where the crown density approaches 100%, various species of moss are the principal understory plant cover.

The climate is typical of foothill conditions in the Puget Sound Basin. The area is at 210 m elevation. The temperatures are moderate and seldom reach the extremes recorded (-18 C to 38C). The average annual precipitation is 136 cm with nearly all of it coming as rain. Ninety percent of the rain falls at a rate of less than 0.25 cm/hr and is concentrated in the winter months. Because of the mild climatic conditions, the soils are seldom frozen. When freezing does occur, it is brief and superficial.

METHODOLOGY

Sampling the components of the ecosystem

Tree components were oven-dried at 70 C to a constant weight.

1. Foliage and branches were sampled separately for the top third of the crown and sampled by middle third and bottom third for the remainder. Current year foliage and branches were removed in the field for separate analysis. Entire samples were retained for weighing. Samples of foliage were taken to obtain the dry weight of a known number of needles so that elemental contents could be expressed on an absolute base.
2. Total dead branches were retained for weighing.
3. The bole was sectioned at 3-m intervals, with 5-cm discs removed, to provide samples of bark and bole wood. Bark was peeled from discs for separate weighing before oven drying. Current year increment of wood was obtained by measuring growth rings and subsequently calculating the volume

and weight represented.

4. Root systems were removed intact with shovel and backhoe. The entire root system was retained and reduced to 10-cm cubes for oven-drying.
5. Sampling was completed on a group of trees that included a normal range of diameter and crown classes. Ten trees occupying 0.004 ha were used to obtain the data presented here.
6. All sampling was completed during October 1965 (before the fall rains).
7. Additional samples were taken from adjacent trees to observe change with time.

Forest floor and *subordinate vegetation* were sampled from both the sample plot and adjacent areas. Data were composited from 40 samples (each sample 2088 cm^2), stratified into Aoo and Ao zones. Subordiante vegetation was harvested from each of these sampling positions.

Soil samples were taken by 15-cm intervals in the top 60 cm of the profile because the soil horizons are quite poorly defined and irregular in depth. This depth encompassed most of the rooting zone. Organic material in the soil was calculated from carbon determinations assuming soil organic matter to be 58% carbon.

Measuring the transfer rates between components of the ecosystem

Litterfall was collected monthly on 2088-cm^2, No. 20-mesh, plastic screens mounted about 15 cm off the ground.

Leaf wash was collected beneath the litter screens to collect both the wash off the foliage while on the tree and off the litter while in the screens.

Filters were placed in these collecting troughs to retain the particulate matter.

Stemflow was collected by a beveled rubber trough placed spirally around the tree. The stemflow was directed into a large collection bottle through plastic tubing from the above trough. A filter was placed in the line to the bottle to retain particulate matter.

A tension lysimeter system was used to study transfer through the forest floor and soil. Individual lysimeter plates were placed directly beneath the forest floor and at approximately 1 m in the soil profile. In this way, the soil solution was collected as it entered into and left the rooting zone.

Uptake by forest vegetation was determined by sampling the current year's growth increment including the foliage, branches, and bole. This was done as part of the biomass study. The continued accumulation of calcium in the foliage and branches after the initial development was determined so that calcium uptake could be calculated (Appendix, Fig. 6).

Chemical analyses of the components of the ecosystem

Soil analyses were handled as described below. Laboratory analyses were performed on soil material passing a 2-mm-mesh screen and oven-dried at 105 C. Values for the elements were corrected for the soil gravel content and bulk density before calculating the weight-per-unit-area data.

1. Nitrogen was determined by standard Kjeldahl digestion and distillation into boric acid.
2. Exchangeable calcium and potassium were determined from an aliquot of neutral, normal, NH_4OAc used to leach the soil.

Following digestion of the leachate, calcium was determined by an EDTA titration using a murexide indicator and Ell's titrometer and colorimeter. Potassium analysis was made on a Beckman DU spectrophotometer with oxy-acetylene flame at a wavelength of 768 mμ .

3. Total phosphorus was determined on soil extract following digestion in 30% H_2O_2 and 36 N H_2SO_4. The level was found colorimetrically by the vanadomolybdophosphoric yellow color method of Jackson (1960).

Vegetative analyses were performed for tree components, subordinate vegetation, and forest floor as follows: tissue was ground to pass a 30-mesh screen in either a Wiley mill or Waring blender and oven-dried at 70 C. One-gram samples of tissue were digested in 30% H_2O_2 with 36 N H_2SO_4 (Naponen, Dries, and O'Brien, 1947). The final digests were 1.8 N with H_2SO_4. Aliquots from this digestion were taken for the individual elemental analyses as described below:

1. Nitrogen was obtained by micro-Kjeldahl distillation into 4% boric acid and titrated with dilute H_2SO_4.
2. Calcium was determined by atomic absorption spectrophotometry using a Ca-Mg hollow cathode lamp, nitrous oxide-acetylene flame, and a wavelength of 4230 mμ.
3. Phosphorus was found colorimetrically by the vanadomolybdophosphoric yellow color method of Jackson (1960).
4. Potassium was obtained by flame emission on a Beckman DU spectrophotometer with oxy-acetylene flame at a wavelength of 768 mμ.

RESULTS AND DISCUSSION

Elemental distribution

The distribution of nitrogen, phosphours, potassium, and calcium in the various components of the ecosystem is listed in Table 1. Associated with this distribution is a large between-tree variation. For example, within the 10 trees taken from a 0.004-ha plot that were harvested for this study, the total mass per tree varied between 1,532 g for the supressed tree S-1 to 197,691 g for the dominant tree D-2--difference of over 100-fold. This same magnitude of variation existed for all the component parts of the tree (Appendix, Table 8). Similarly, a corresponding variation was found in the elemental composition of the trees (Appendix, Tables 9, 10, 11, and 12). This variation reflects the normal corwn class development typical of an even-aged stand of Douglas-fir. Since the trees were removed from a plantation of relatively uniform spacing, the variation described is undoubtedly less than that found in natural stands.

The variation in the biomass and mineral composition was also determined for the other components of the ecosystem. The largest variation occurred in the subordinate vegetation. With samples taken from areas of 2088 cm^2, a coefficient of variation (CV) of 132% was found. From the same sampling areas, the CV of the biomass of the forest floor was 51% in the Ao and 47% in the Aoo layers.

Utilizing bulk samples of 1061 cc, the CV of the soil nitrogen was found to be 20% at the 0-7.5 cm depth (A_1 horizon), 21% at the 7.5-15 cm depth (B_{21} horizon), 17% at the 23-30 cm depth (B_{22} horizon), and 41% at the 52.5-60 cm depth (C horizon) (Irby, 1967). These values probably reflect variation in the organic matter content.

As seen in Table 1 and summarized in Table 2, from 10 to 15% of the total mass and mineral composition of the tree is located within the roots and that part of the stump below ground level. It is apparent from these data that the roots cannot be ignored in mineral distribution, biomass, and mineral cycling studies because they represent the second largest tree component.

Equally significant is the mineral composition of the bark. Although the total mass is considerably less than that found in the roots, the mineral elemental accumulation is very high.

The distribution of mineral elements within the ecosystem is summarized in Table 3. These data show that the subordinate vegetation is of minimal importance in the overall distribution of the mineral elements. The largest percentage accumulation is found for potassium. In the 35 years of development, the vegetation has accumulated 46% of the available ionic potassium and 28% of the organic and ionic calcium contained within the ecosystem. During this same period, 10% of the nitrogen and 2% of the available phosphorus have accumulated in the vegetation.

The elemental distribution data described above represent a redistribution that has occurred since the establishment of the stand. To evaluate this redistribution on an annual basis, it is necessary to also assess the transfer rates between components.

Cycling between components

The transfer of nitrogen, phosphorus, potassium, and calcium has been measured between the three major components of the ecosystem. These measurements include: 1) uptake—transfer from the soil to the tree;

2) return—transfer from the tree to the forest floor; and 3) leaching from the forest floor to the soil. Collectively, these measurements describe the overall elemental cycle between the tree, forest floor, and soil components. In addition, measurements were made of the input into the cycle by precipitation and loss from the cycle by leaching beyond the rooting zone.

The rate of annual transfer of the above mineral elements is described in Table 4. From these data, it can be seen that the cycle within the ecosystem is far more significant in mineral transfer than the additions to or losses from the cycle by precipitation and leaching. The data on elemental additions to the cycle by precipitation compare closely to, but slightly lower than, those observed by Moodie (1964) at a number of sites in western Washington. Since Moodie's collections were all made within or near populated areas, this small discrepancy is explainable. The losses by leaching closely approximate similar measurements made at this study area (Cole and Gessel, 1965) and at similar ecosystems in western Washington (Cole, Gessel, and Held, 1961).

The current annual uptake of nitrogen for ecosystem was found to be 38.8 kg/ha. In all probability this also represents a minimum nitrogen requirement for the forest stand since an adjacent nitrogen fertilizer study resulted in a substantial growth response. The uptake is slightly less for both potassium and calcium and appreciably less for phosphorus.

The elemental uptake measured at this area is not appreciably different than that observed in other ecosystems. For example, it was estimated by Remezov (1965) that a coniferous forest has a maximum annual uptake per hectare of 50 - 60 kg of nitrogen, 6 - 12 kg of phosphorus, 20 - 40 kg of potassium, and 40 - 50 kg of calcium. Ovington (1959) found the maximum annual uptake of *Pinus sylvestris* occurred at age 30, approximately the same age as the forest in our study. The annual per hectare uptake by this species appears to be somewhat higher than that of Douglas-fir, 78 kg of nitrogen, 7 kg of phosphorus, 3 kg of potassium, and 41 kg of calcium. For Douglas-fir growing on low site glacial soils in western Washington, Heilman and Gessel (1963) found an annual nitrogen uptake of 25 kg/ha. The distribution of the uptake in this study into the various component parts of the tree is listed in Table 5.

The return of elements from the forest to the forest floor was stratified into three component parts: litterfall, stamflow, and leaf wash. The return of elements by leaf wash was adjusted to take into consideration elemental additions from the atmosphere during periods of precipitation. The general mobility of the various mineral elements is demonstrated in these data. For example, 10% of the nitrogen, 50% of the phosphorus, 71% of the potassium, and 22% of the calcium is returned in the leaf and litter wash. The phosphorus percentage could be in error because of the small quantities involved. This high transfer rate in leaf wash has been observed in many other ecosystems (Will, 1955, 1959; Tamm, 1951; Madgwick and Ovington, 1959).

By comparing the uptake data with total return, a general indication of the rate of elemental turnover by the forest component of the ecosystem can be established. Based on the data of Table 5, a turnover progression of Ca>K>N>P is evident in this particular ecosystem. It is probable that potassium and calcium would be reversed in the above progression if the high calcium accumulation in the bark had been included in the calculation.

By combining these transfer data with the previously discussed distribution data, annual cycling diagrams were constructed for the four mineral elements (Figs. 1, 2, 3, and 4). The accumulation within each component is represented as a circle while the transfer rate between components is represented as an arrow. The area of each circle reflects the magnitude of accumulation while the width of each arrow indicates the magnitude of the transfer rate.

These diagrams integrate total transfer between components for an entire year. These transfer rates fluctuate through wide extremes during the course of the year. For example, Fig. 5 shows the return of nitrogen, calculated on a daily basis by way of litterfall, precipitation, and leaf wash. These measurements were taken from May to mid-November 1967 for litterfall and from July to mid-November for precipitation and leaf wash. The frequency of sampling during this period is indicated on the time axis of Fig. 5. The monthly pattern of elemental movement through the forest floor and past the rooting zone at the 90-cm depth was previously reported for this ecosystem (Cole and Gessel, 1965; Gessel and Cole, 1965).

Accumulation and depletion rates between components of the ecosystem

Accumulation of a specific element within any component of the ecosystem can only occur when the input into the component exceeds the output. For a given component, the absolute difference between the input and output during a given period of time defines the rate of accumulation. This rate can also be quantitized by measuring the elemental flux within a component during a given period of time. A systematic sampling and resampling approach to measuring rate of accumulation is very insensitive for the larger components of the ecosystem, particularly where a high coefficient of variation is also involved. For example, the maximum senstivity that can be obtained for fluxes in soil nitrogen by assessing quantities in the soil is 50 kg/ha. Therefore, to assess the rate of accumulation, particularly where large masses are involved, it is desirable to directly measure the input and output of the element from each component of the ecosystem.

In evaluating the mineral cycle at Cedar River, the input and output measurements were made for each component as described in the previous section. Accumulation values for the different elements have been calculated from these transfer rates. Table 6 indicates the rate of elemental accumulation into the major components of the ecosystem from this input-output calculation. Additions to the ecosystem from the atmosphere and losses from the ecosystem by leaching are included in the calculations for this table.

For this specific year, a sizable annual accumulation of all four elements is indicated in the tree and forest floor components of the ecosystem. This accumulation is at the expense of the elemental capital of the soil. These data suggest that a depletion at the rate of 34.6 kg/ha of nitrogen, 6.3 kg/ha of phosphorus, 19.9 kg/ha of potassium, and 11.5 kg/ha of calcium is occurring annually in the soil. If this rate continued the soil could rapidly become depleted of these mineral elements.

Switzer, Nelson, and Smith (1966) reported on average annual nitrogen accumulation for poor site *Pinus taeda*. Approximately 5.6 kg/ha was accumulated during the first 30 years of growth, while 1.7 kg/ha was retained during the next 30 years development.

By comparing the elemental uptake to the elemental capital in the soil, a calculation on the rate of utilization was made (Table 7). It is evident from these data that potassium and calcium are currently being depleted from the soil at a far higher rate than nitrogen and phosphorus. It should be remembered, however, that both nitrogen and phosphorus values represent the total soil capital while the potassium and calcium values are for the exchangeable components only.

A further indication of the significance of the depletion of the mineral elements in the soil has been calculated from the above data (Table 7). It is the purpose of this calculation to indicate the trends of this redistribution and depletion pattern. Any absolute evaluation of depletion, accumulation, and utilization would have to include at least two additional parameters of the ecosystem:

1. Changes in the transfer rate between components of the ecosystem with time. Such changes would certainly be expected over the life span of the forest community. The redistribution data reported above would also indicate that the relationship between components must be changing with time.
2. Addition of elements in ionic form to the ecosystem through such processes as nitrogen fixation, mineral solubility, and organic matter mineralization.

Assuming, however, that elemental transfer does remain constant with time, it is possible to calculate the time required for total soil depletion to occur. By comparing the annual uptake to the elemental capital in the soil, a first approximation can be made on the number of years this supply will last (static supply in Table 7).

However, as we have already demonstrated, this depletion rate is somewhat augmented through addition by rainfall and the reutilization of elements by mineral cycling. In addition, the supply is further depleted by leaching beyond the rooting zone. Considering these three factors, a more realistic calculation on the elemental supply in the soil can be made (cyclic supply in Table 7). It is suggested from these data that the supply of soil potassium could become critical in only 12 years, a period far shorter than the life expectancy of the forest. In all probability this will not occur for the two reasons discussed earlier.

However, such calculations do have a definite utility in understanding the dynamics of a forest community. From the calculations of Table 7, the future redistribution patterns of the mineral elements within the ecosystem can be estimated. By measuring the actual redistribution pattern in some future year this calculation can be checked. From the differnce between the calculated quantities developed from Table 7 and the actual quantities established from resampling, it should be possible to establish the rate and nature of elemental input into the ecosystem and to develop a mathematical model of the efficiency of elemental utilization.

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Table 1. Distribution of N, P, K, Ca, and organic matter (kg/ha) in a second-growth Douglas-fir ecosystem

Component		N	P	K	Ca	Organic matter
TREE						
Foliage	current	24	5	16	7	1,990
	older	78	24	46	66	7,107
Branches	current	4	1	3	2	513
	older	40	9	32	65	13,373
	dead	17	2	3	39	8,145
Wood	current	10	2	10	4	7,485
	older	67	7	42	43	114,202
Bark		48	10	44	70	18,728
Roots		32	6	24	37	32,986
Total tree		320	66	220	333	204,529
SUBORDINATE VEGETATION		6	1	7	9	1,010
FOREST FLOOR						
Branches		5	1	4	8	1,423
Needles		35	4	5	27	3,005
Wood		14	2	8	17	6,345
Humus		121	19	15	85	11,999
Total forest floor		175	26	32	137	22,772
SOIL						
0-15 cm		809	1,167	79	313	38,372
15-30 cm		868	1,195	66	196	36,935
30-45 cm		761	980	52	152	28,290
45-60 cm		371	536	37	80	7,955
Total soil		2,809	3,878	234	741	111,552
TOTAL ECOSYSTEM		3,310	3,971	493	1,220	339,863

Table 2. Distribution of N, P, K, and Ca between the major components of the second-growth Douglas-fir forest

Ecosystem component	N		P		K		Ca	
	Kg/ha	% of total	kg/ha	% of total	kg/ha	% of total	kg/ha	% of total
Foliage	102	31.9	29	43.9	62	28.2	73	21.9
Branches	61	19.1	12	18.2	38	17.3	106	31.8
Wood	77	24.0	9	13.6	52	23.6	47	14.1
Bark	48	15.0	10	15.2	44	20.0	70	21.0
Roots	32	10.0	6	9.1	24	10.9	37	11.2
Total	320		66		220		333	

Table 3. Distribution of N, P, K, and Ca within the major components of the ecosystem

Ecosystem component	N		P		K		Ca	
	kg/ha	% of total	kg/ha	% of total	kg/ha	% of total	kg/ha	% of total
Forest	320	9.7	66	1.7	220	44.6	333	27.3
Sub vegetation	6	0.2	1	0.1	7	1.4	9	0.7
Forest floor	175	5.3	26	0.6	32	6.5	137	11.2
Soil	2809*	84.8	3878*	97.6	234**	47.5	741**	60.8
Total	3310		3971		493		1220	

* Total
** Exchangeable with *p*H 7 ammonium acetate

Table 4. Annual transfer of N, P, K, and Ca (kg/ha) between components of the ecosystem

	N	P	K	Ca
Input (Precipitation)	1.1	T*	0.8	2.8
Uptake by forest	38.8	7.23	29.4	24.4
Total return to forest floor	16.4	0.60	15.8	18.5
Leached from forest floor	4.8	0.95	10.5	17.4
Leached beyond rooting zone	0.6	0.02	1.0	4.5

*Trace

Table 5. Annual uptake and return of N, P, K, and Ca (kg/ha) by the second-growth Douglas-fir forest

Component	N	P	K	Ca
Annual uptake				
Foliage	24.3	4.7	16.2	17.8
Branches	4.2	0.8	2.7	2.6
Bole	10.3	1.7	10.5	4.0
Total	38.8	7.2	29.4	24.4
Annual return				
Litter fall	13.6	0.2	2.7	11.1
Stemflow	0.2	0.1	1.6	1.1
Leaf wash	1.5	0.3	10.7	3.5
Total	15.3	0.6	15.0	15.7

Table 6. Annual accumulation of N, P, K, and Ca (kg/ha) within the major components of the total ecosystem

Component	N	P	K	Ca
Forest	23.5	6.6	14.4	8.7
Forest floor	11.6	-0.4	5.3	1.1
Soil	-34.6	-6.3	-19.9	-11.5

Table 7. Utilization of N, P, K, and Ca from the soil by the second-growth Douglas-fir Forest

Element	% yearly uptake*	Static supply (yr)	Cyclic supply (yr)**
N	1.4	73	125
P	0.2	537	582
K	12.5	8	12
Ca	3.3	30	64

*Yearly uptake divided by total in the ecosystem

**Includes input by precipitation and return by the litter, stemflow, and wash

APPENDIX

Table 8. Distribution of dry matter (g dry wt) between components of the individual trees on a 0.004-ha plot.

	Tree number by crown class*										
Tree component	S-1	I-1	I-2	I-3	C-1	C-2	C-3	C-4	D-1	D-2	Totals
Current foliage	18	62	32	101	978	445	1100	1976	2169	2068	8949
Older foliage	77	390	241	514	2629	2338	4262	6893	5385	9232	31961
Total foliage	95	452	273	615	3607	2783	5362	8869	7554	11300	40910
Current branches	4	28	11	28	215	164	263	501	589	508	2311
Older branches	145	751	890	924	5394	3749	5975	16578	12987	12743	60136
Total branches	149	779	901	952	5609	3913	6238	17079	13576	13251	62447
Dead branches	68	963	1406	1158	4985	3902	4072	7668	7215	5190	36627
Current wood	1	206	182	238	3397	1509	5024	7383	6214	9507	33660
Older wood	568	10292	9497	13592	73219	39093	67775	86308	105770	107428	513543
Total wood	569	10498	9679	13830	76616	40602	72799	93691	111984	116935	547203
Bark	166	1816	1356	2082	14351	6673	10963	11836	17999	16977	84219
Total aerial	1047	14508	13615	18637	105168	57873	99434	139143	158328	163653	771406
Large roots and stumps	450	2260	1653	2755	14086	10804	17900	28186	32481	33191	143766
Small roots	35	266	129	160	614	327	749	882	559	847	4568
Total sub-aerial	485	2526	1782	2915	14700	11131	18649	29068	33040	34038	148334
Total tree	1532	17034	15397	21552	119868	69004	118083	168211	191368	197691	919740

*S-1 is suppressed
I-1, I-2, and I-3 are intermediate
C-1, C-2, C-3, and C-4 are codominant
D-1 and D-2 are dominant

Table 9. Distribution of nitrogen (g dry wt) between components of the individual trees on a 0.004-ha plot

	Tree number by crown class*										
Tree component	S-1	I-1	I-2	I-3	C-1	C-2	C-3	C-4	D-1	D-2	Totals
Current foliage	0.19	0.67	0.29	1.07	11.90	4.88	12.12	24.26	28.59	25.31	109.28
Older foliage	0.85	4.13	2.68	5.29	26.58	24.46	45.21	77.13	53.82	109.81	349.96
Total foliage	1.04	4.80	2.97	6.36	38.48	29.34	57.33	101.39	82.41	135.12	459.24
Current branches	0.03	0.18	0.08	0.22	1.66	1.18	1.95	4.21	5.24	4.06	18.81
Older branches	0.62	2.48	2.67	2.96	15.64	11.62	16.13	48.08	38.96	40.78	179.94
Total branches	0.65	2.66	2.75	3.18	17.30	12.80	18.08	52.29	44.20	44.84	198.75
Dead branches	0.24	3.66	3.94	3.82	10.47	8.58	7.74	12.27	13.71	10.38	74.81
Current Wood	--	0.31	0.27	0.36	4.42	2.26	6.53	9.60	7.46	15.21	46.42
Older wood	0.46	5.99	5.54	6.56	43.93	23.46	47.44	51.78	52.88	64.46	302.50
Total wood	0.46	6.30	5.81	6.92	48.35	25.72	53.97	61.38	60.34	79.67	348.92
Bark	0.56	5.08	4.88	6.04	28.70	16.68	28.50	33.14	46.80	45.84	216.22
Total aerial	2.95	22.50	20.35	26.32	143.30	93.12	165.62	260.47	247.46	315.85	1297.94
Large roots and stumps	0.45	2.26	1.32	1.65	14.09	8.64	10.74	25.37	32.48	36.51	133.51
Small roots	0.10	0.72	0.26	0.34	1.72	0.72	1.72	1.76	1.34	1.18	9.86
Total sub-aerial	0.55	2.98	1.58	1.99	15.81	9.36	12.46	27.13	33.82	37.69	143.37
Total tree	3.50	25.48	21.93	28.31	159.11	102.48	178.08	287.60	281.28	353.54	1441.31

*S-1 is suppressed.
I-1, I-2, I-3 are intermediate.
C-1, C-2, C-3, C-4 are codominant.
D-1, D-2 are dominant.

Table 10. Distribution of phosphorus (g dry wt) between components of individual trees on a 0.004-ha plot

	Tree number by crown class*										
Tree component	S-1	I-1	I-2	I-3	C-1	C-2	C-3	C-4	D-1	D-2	Totals
Current foliage	0.04	0.09	0.06	0.21	1.91	0.94	2.47	4.53	5.80	4.81	20.86
Older foliage	0.27	0.68	0.56	1.52	7.58	6.11	13.67	24.93	18.63	31.85	105.80
Total foliage	0.31	0.77	0.62	1.73	9.49	7.05	16.14	29.46	24.43	36.66	126.66
Current branches	0.01	0.04	0.02	0.04	0.32	0.24	0.40	0.81	1.07	0.84	3.79
Older branches	0.10	0.49	0.44	0.46	3.05	2.27	3.70	13.43	9.71	8.86	42.51
Total branches	0.11	0.53	0.46	0.50	3.37	2.51	4.10	14.24	10.78	9.70	46.30
Dead branches	0.03	0.31	0.30	0.38	1.05	0.70	0.86	1.99	1.73	1.35	8.70
Current wood	-	0.01	0.02	0.02	0.93	0.35	1.53	1.55	1.37	2.04	7.82
Older wood	0.04	0.67	0.95	0.88	4.76	2.54	4.07	5.61	6.88	6.98	33.38
Total wood	0.04	0.68	0.97	0.90	5.69	2.89	5.60	7.16	8.25	9.02	41.20
Bark	0.11	0.64	0.93	1.04	7.18	3.57	6.91	7.69	8.55	10.70	47.32
Total aerial	0.60	2.93	3.28	4.55	26.78	16.72	33.61	60.54	53.74	67.43	270.18
Large roots and stumps	0.16	0.58	0.58	0.76	2.96	1.62	2.68	5.50	5.03	4.81	24.68
Small roots	0.04	0.16	0.14	0.10	0.43	0.19	0.50	0.56	0.32	0.59	3.03
Total sub-aerial	0.20	0.74	0.72	0.86	3.39	1.81	3.18	6.06	5.35	5.40	27.71
Total tree	0.80	3.67	4.00	5.41	30.17	18.53	36.79	66.60	59.09	72.83	297.89

*S-1 is suppressed
I-1, I-2, and I-3 are intermediate
C-1, C-2, C-3, and C-4 are codominant
D-1 and D-2 are dominant

Table 11. Distribution of potassium (g dry wt) between components of individual trees on a 0.004-ha plot.

	Tree number by crown class*										
Tree component	S-1	I-1	I-2	I-3	C-1	C-2	C-3	C-4	D-1	D-2	Totals
Current foliage	0.16	0.57	0.17	0.96	7.65	3.33	7.48	14.75	19.83	17.70	72.60
Older foliage	0.57	2.24	0.97	3.42	21.42	16.23	22.48	40.71	39.28	60.69	208.01
Total foliage	0.73	2.81	1.14	4.38	29.07	19.56	29.96	55.46	59.11	78.39	280.61
Current branches	0.03	0.20	0.05	0.17	1.13	0.98	1.23	2.70	2.89	2.94	12.32
Older branches	0.34	1.78	1.35	1.85	14.56	10.68	12.96	35.14	31.82	33.13	143.61
Total branches	0.37	1.98	1.40	2.02	15.69	11.66	14.19	37.84	34.71	36.07	155.93
Dead branches	0.06	0.25	0.21	0.25	1.34	0.55	1.06	3.53	3.10	2.39	12.74
Current wood	-	0.18	0.19	0.20	5.47	1.69	8.39	10.04	8.64	12.64	47.44
Older wood	0.26	3.60	2.71	3.40	26.36	11.73	27.11	32.80	40.19	39.75	187.91
Total wood	0.26	3.78	2.90	3.60	31.83	13.42	35.50	42.84	48.83	52.39	235.35
Bark	0.42	2.89	2.60	3.33	28.84	12.28	29.38	35.39	41.40	39.39	195.92
Total aerial	1.84	11.71	8.25	13.58	106.77	57.47	110.09	175.06	187.15	208.63	880.55
Large roots and stumps	0.36	1.83	1.34	2.09	9.72	4.54	10.74	22.27	26.63	23.23	102.75
Small roots	0.06	0.40	0.23	0.26	1.07	0.43	1.31	1.30	0.96	0.91	6.93
Total sub-aerial	0.42	2.23	1.57	2.35	10.79	4.97	12.05	23.57	27.59	24.14	109.68
Total tree	2.26	13.94	9.82	15.93	117.56	62.44	122.14	198.63	214.74	232.77	990.23

*S-1 is suppressed
I-1, I-2, and I-3 are intermediate
C-1, C-2, C-3, and C-4 are codominant
D-1 and D-2 are dominant

Table 12. Distribution of calcium (g dry wt) between components of individual trees on a 0.004-ha plot.

	Tree number by crown class*										
Tree component	S-1	I-1	I-2	I-3	C-1	C-2	C-3	C-4	D-1	D-2	Totals
Current foliage	0.05	0.24	0.09	0.37	3.06	1.54	4.19	10.32	7.35	5.38	32.59
Older foliage	0.63	3.07	1.72	3.88	16.00	20.08	39.35	81.40	37.86	91.03	295.02
Total foliage	0.68	3.31	1.81	4.25	19.06	21.62	43.54	91.72	45.21	96.41	327.61
Current branches	0.02	0.10	0.04	0.10	0.92	0.65	1.04	1.94	2.44	2.14	9.39
Older branches	1.02	3.76	4.96	4.35	24.00	17.66	32.03	80.24	57.79	68.30	294.11
Total branches	1.04	3.86	5.00	4.45	24.92	18.31	33.07	82.18	60.23	70.44	303.50
Dead branches	0.53	5.10	7.61	6.26	21.44	20.68	19.02	32.97	33.69	26.52	173.82
Current wood	-	0.10	0.08	0.11	2.68	1.46	2.56	3.10	3.29	4.85	18.23
Older wood	0.39	5.04	4.18	5.84	25.63	17.20	23.72	39.70	37.02	34.38	193.10
Total wood	0.39	5.14	4.26	5.95	28.31	18.66	26.28	42.80	40.31	39.23	211.33
Bark	1.34	8.55	8.22	11.16	44.20	41.64	39.80	38.11	65.34	57.21	315.57
Total aerial	3.98	25.96	26.90	32.07	137.93	120.91	161.71	287.78	244.78	289.81	1331.83
Large roots and stumps	1.12	4.88	3.88	3.22	18.17	19.88	12.71	20.29	40.28	31.86	156.29
Small roots	0.13	0.95	0.44	0.37	1.77	1.16	1.70	1.50	1.66	2.34	12.02
Total sub-aerial	1.25	5.83	4.32	3.59	19.94	21.04	14.41	21.79	41.94	34.20	168.31
Total tree	5.23	31.79	31.22	35.66	157.87	141.95	176.12	309.57	286.72	324.01	1500.14

*S-1 is suppressed
I-1, I-2, and I-3 are intermediate
C-1, C-2, C-3, and C-4 are codominant
D-1 and D-2 are dominant

Table 13. Morphological, chemical and physical characteristics of the Everett Soil.

Depth	Description
2½ - 0 cm	- Acid, dark brown partially decomposed forest litter
0 - 2½ cm	- Dark brown (10YR 3/3) sandy loam; very weak fine granular structure; friable and readily permeable; scattered concretions; clear wavy boundary; many roots; pH 5.4.
2½ - 5 cm	- Dark yellowish brown (10YR 4/4) sandy loam; very weak fine granular structure; loose; clear wavy boundary; many roots; pH 5.5.
5 -30 cm	- Yellowish brown (10YR 5/4) loamy sand; single grain structure; loose; abrupt wavy boundary; roots present; pH 5.65.
30 - 60 cm	- Yellowish brown (10YR 5/4) gravelly sand; single grain structure; loose; few roots; pH 5.85.

Chemical and Physical Characteristic Data

Depth	% > 2mm.	% Water by weight at:		Bulk Density	% Organic Matter
		0.1atm.	15 atm.		
0 - 2½	50.9	32.2	4.7	0.80	8.25
2½ - 5	60.1	28.3	3.0	1.05	2.54
5 - 30	58.5	14.1	2.6	1.40	1.86
30 - 60	79.0	8.8	1.6	1.77	0.30

Depth	CEC	Exchang. Cations (me/100g)			Base Sat.	% N
		K	Ca	Mg	%	
0 - 2½	10.83	0.25	1.88	2.10	38.8	0.15
2½ - 5-30	4.07	0.08	0.25	0.09	10.6	0.025
30 - 60	1.10	0.002	0.13	0.08	19.8	0.004

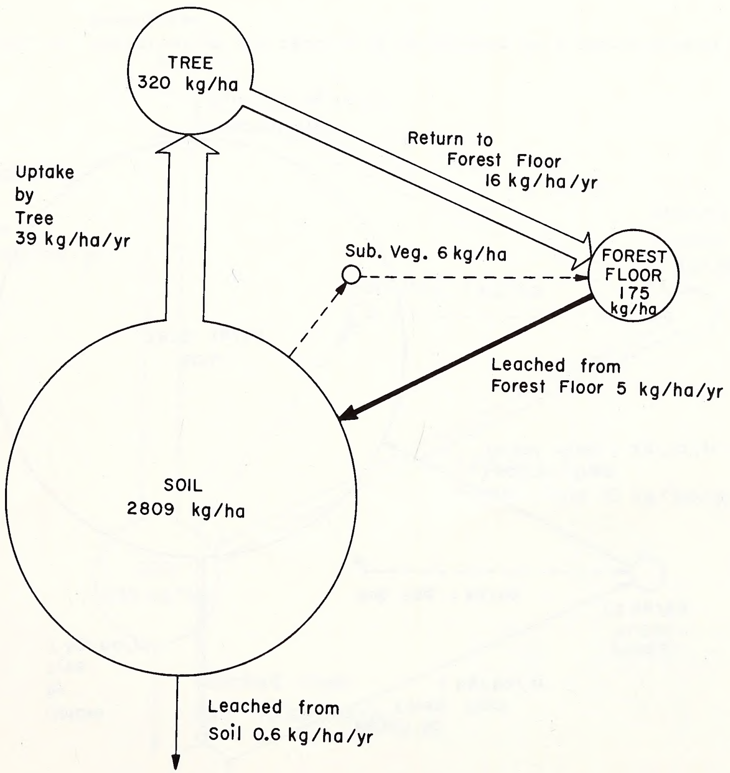

Fig. 1. Distribution and cycling of nitrogen in a second-growth Douglas-fir ecosystem.

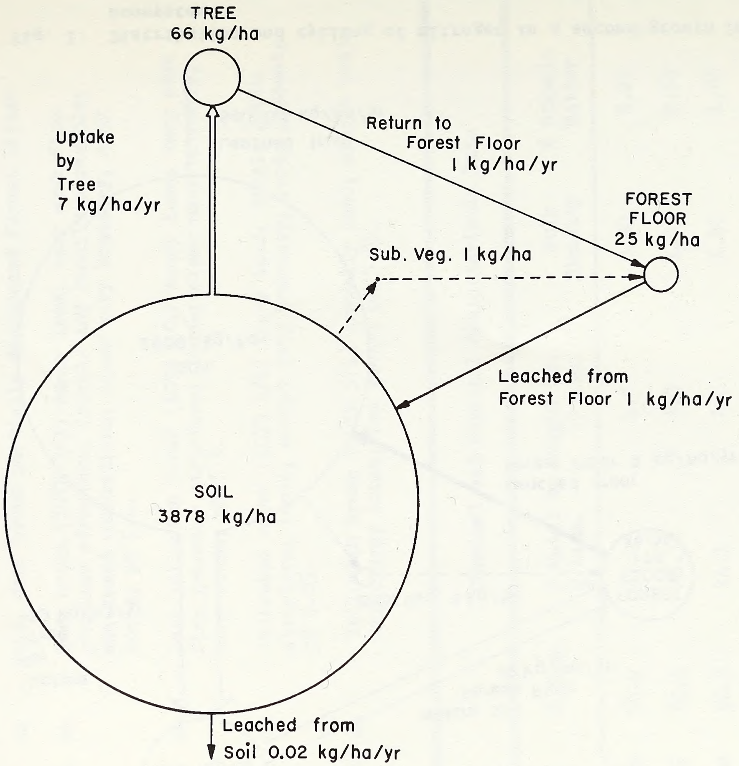

Fig. 2. Distribution and cycling of phosphorus in a second-growth Douglas-fir ecosystem.

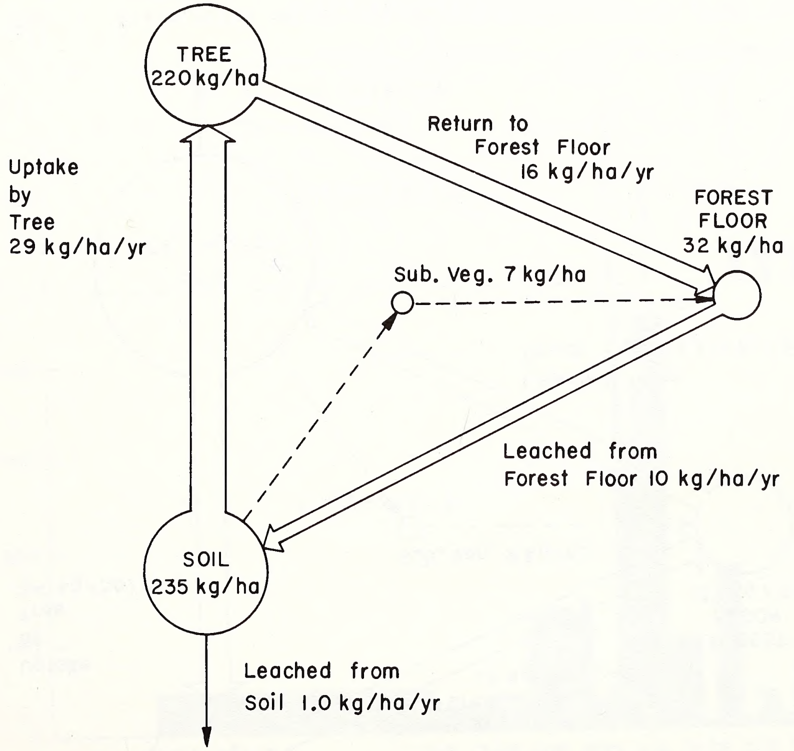

Fig. 3. Distribution and cycling of potassium in a second-growth Douglas-fir ecosystem.

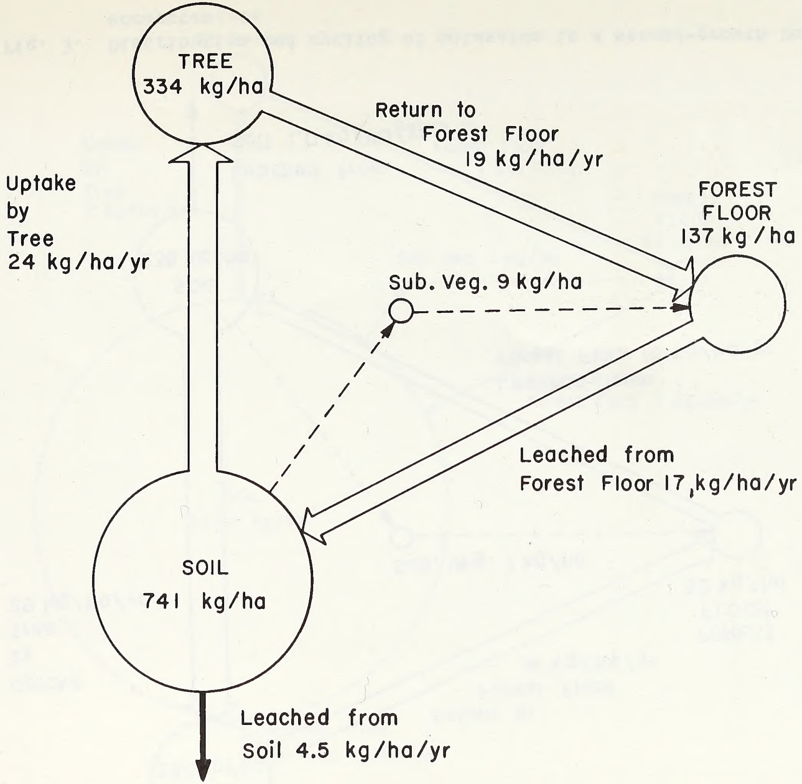

Fig. 4. Distribution and cycling of calcium in a second-growth Douglas-fir ecosystem.

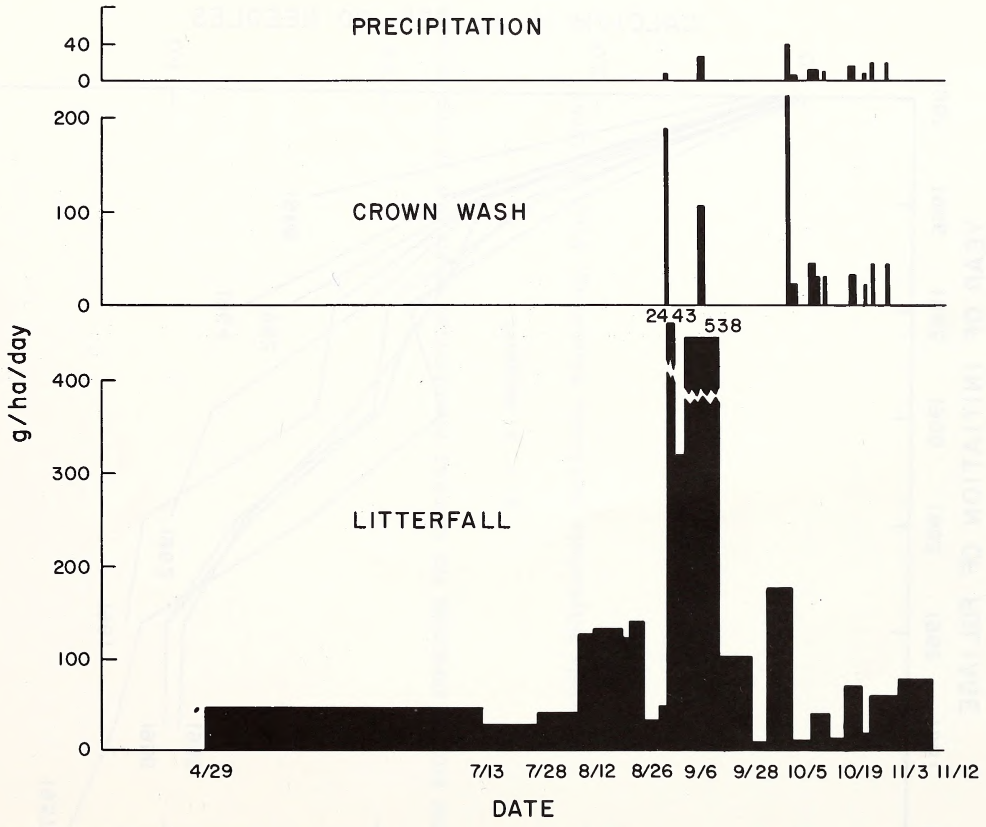

Fig. 5. Daily nitrogen return by litterfall, crown wash, and precipitation.

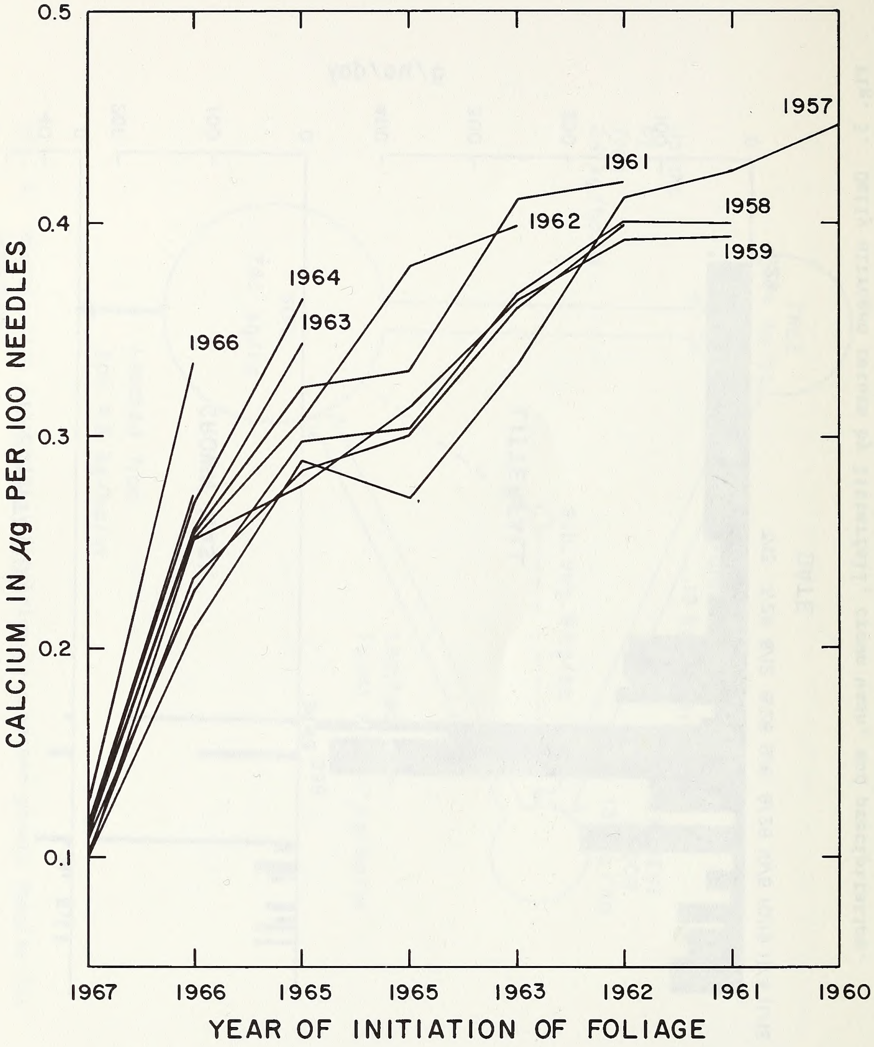

Fig. 6. Increase in foliar calcium with foliage age by whorls.

SOME FACTORS AFFECTING THE VERTICAL DISTRIBUTION OF FOLIAGE IN PINE CANOPIES

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INTRODUCTION

During the past two decades the biological productivity of forests has received increasing attention. Many investigators have cataloged the weights of different portions of the forest biomass of a wide range of forest types (Ovington, 1962). More recently there has been a trend towards considering the forest as a dynamic, complex production system (Olson, 1965). It is with this trend in mind that the ideas in this paper have been developed.

Many foresters have been interested in the relative contributions of different fractions of the tree canopy to the growth of stems. The studies reviewed by Moller (1960) and by Staebler (1963) have mostly been based on the partial removal of different fractions of the canopy as measured by bole length. Only Ladefoged (1946) and Hall (1965) have attempted to measure the distribution of foliage within the canopy as related to stem growth. Hall (1965) noted that foliage distribution within pine crowns varies greatly among trees. Similar variations were presented by Ovington and Madgwick (1959).

Recent intensive research on the biological productivity of stands of vegetation has led to a wider understanding of the distribution of foliage, the relationship between foliage amount and light penetration, and the general relationship between light intensity and photosynthesis of leafy canopies (Saeki, 1959, de Wit, 1965).

The purpose of this paper is to present information on factors affecting foliage distribution within red pine canopies.

EXPERIMENTAL DATA

The data used in this paper were all collected from red pine (Pinus resinosa) trees growing near Warrensburg, New York. In the course of detailed studies of the biomass of two, thirty-year-old plantations (Madgwick, 1962, 1964a) four potassium deficient and three non-deficient trees were sampled in detail. The trees ranged in height from 5 to 15 meters, carried thirteen to seventeen live branch whorls, and ranged from dominant to intermediate in crown class. The canopies of the seven trees were carefully separated into needles and branches by whorls. The needles were further divided according to their age. All material was weighed after oven-drying at 80°C. Additional information collected included annual height increments as measured by distances between successive branch whorls, the number of needle bearing shoots per whorl, and the oven-dry weights of samples of fifty needles of each age class of needles from every third whorl in each canopy. Further details of experimental methods have been presented elsewhere (Madgwick, 1962).

In connection with a further study in the same area (Madgwick, 1964b) data were collected from another 26 open-grown nine-year-old trees on leader length, number of branches, and needle mass on an average branch, from the topmost whorl.

FOLIAGE DISTRIBUTION WITHIN CROWNS

The relative distribution of needle mass by whorls for each of the seven trees is illustrated in Fig. 1 using data for the total weight of needles per whorl. The data support the views of Hall (1965), based on analysis of four red pine canopies, that foliage distribution within crowns is extremely erratic. Little more can be said than that the foliage amount is a minimum near the apex and near the base of the live canopy with a tendency for greater foliage concentration in mid-canopy regions. Even so, some whorls in mid-crown positions were poorly developed and carried relatively few needles. Although it would be possible to approximate foliage distribution by some flexible statistical distribution, variation is so great that little would be gained. In order to understand the distribution of foliage within the canopy we must obviously know more about the internal relationship within the canopy affecting foliage development.

FACTORS AFFECTING FOLIAGE DEVELOPMENT WITHIN CANOPIES

In an attempt to explain the erratic distribution of foliage within canopies, a number of factors have been isolated.

Initial development of branch whorls. The data for all 33 sample trees were combined to demonstrate the relationship between leader growth and foliage weight on the topmost whorl (Fig. 2). Foliage on the uppermost whorl increased logarithmically from 4.4 gm. on trees with an 18 cm. leader to 91 gm. on trees with a 66 cm. leader. The logarithm of leader length accounted for 84 per cent of the variation in logarithm of needle weight on the topmost whorl. Both leader growth and needle mass reflect the effects of soil nutrient and moisture supply as well as climatic conditions. However, knowing leader growth permits the prediction of initial needle weight on the one-year-old branch whorl.

Subsequent development of branch whorls. Inspection of the data indicated that growth of at least the uppermost four branch whorls remained approximately constant both within and between trees. Plotting the one-year-needle weight on one whorl against that on the next lower whorl (Fig. 3) indicated growth from whorl to whorl of 160 ± 15 per cent. By combining this information with a knowledge of leader growth, it is possible to predict growth for the first few years.

The effects of shading on lower branch whorls. Further development of the branch whorl will be affected by the degree of shading. In the present instance some measure of the shading effect on lower branch whorls may be obtained by observing changes in needle size within the canopy (Fig. 4). Using needle weight on the topmost whorl as a base, needle weight was linearly related to the fraction of total needle mass on the tree above a particular sample branch. At the base of the canopy the weight of the average individual needle was only 36 to 50 per cent of the weight of the average individual needle on the topmost whorl. Further effects of shading on total weights of needles on a branch may be postulated as a result of the death of growing points, the increased ratio of respiring branch tissue to photosynthesing needle tissue, and the like.

Increased shading of lower branches leads eventually to death but no clear cut-off point is indicated in terms of needle characteristics. The weights of individual needles, needles per live shoot, needles per whorl, and the ratio of total needle weight to total branch weight for the lowest live whorl all varied markedly from tree to tree (Table 1).

The longevity of needles. Total needle mass on the tree is affected not only by the rate of production of current needles but also by longevity of needles once produced. Potassium fertilization has been reported to increase needle longevity (Heiberg, et al., 1964). Data presented in Fig. 5 have been corrected for differences in weights of individual needles from year to year and for the differential loss of older needles due to branch death at the base of the canopy. The four potassium deficient trees lost their needles by the end of the third year while the three non-deficient trees held almost a full complement of needles for the same period, serious loss not occurring until the fifth year.

DEVELOPMENT OF A MODEL OF CROWN GROWTH

In order to determine to what extent the factors isolated describe the distribution of foliage within the canopy, a computer program was written to simulate crown growth. Variables included were:

1. A logarithmic relationship between height growth and foliage weight on the topmost whorl
2. A constant potential growth rate from year to year
3. Factors to account for needle fall as needles aged
4. A shading effect

First approximations of the numerical values of variables one to three for each sample tree could be obtained from the data presented in Figs. 2, 3, and 5.

The effect of shading was thought to be more complex than that suggested by the data in Fig. 4 so a more flexible shading effect was postulated. Foliage growth on any particular whorl was made to vary continuously, but not necessarily linearly, with the relative amount of foliage above the whorl in question.

For each of the four potassium-deficient trees, estimated values of foliage distribution were calculated. In order to compare these values with the actual weights, logarithmic transformations were applied since crown growth is basically logarithmic and relative errors were thought to be more important than absolute errors. By suitable manipulation of the arithmetic values of the variables the growth model explained up to 64 per cent of the variation of the logarithm of foliage weight.

The present model makes a large number of assumptions concerning the nature of crown development. For instance, the relative growth rate of branch whorls is assumed constant irrespective of tree age and seasonal variations in weather conditions; needle longevity is assumed unaffected by shading within the canopy; and the like. However, in view of the fact that growth of the whorls was projected forward up to seventeen years to estimate current foliage distribution and the simplicity of the model, agreement between calculated and expected needle mass is encouraging.

In order to decide whether crown growth has been realistically simulated on the computer it is necessary to decide on an acceptable degree of agreement between the theoretical and actual data. However, I believe that we have sufficient evidence to suggest that attempting to model crown development is worthwhile and that with further refinement and extension of such a model, we may be able to effectively simulate tree growth on a computer. Moreover, we may be able to develop a concept of an efficient tree which could significantly influence selection procedures in genetic tree improvement.

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Table 1. Some characteristics of the lowest live branch whorl on seven sample trees

Factor	Minimum	Maximum	Average
Total weight of needles g.	2.1	324.7	55.6
Total weight of one-year needles g.	1.7	47.9	10.9
Total needle weight per live shoot g.	0.4	6.6	2.1
One-year needle weight per live shoot g.	0.3	1.7	0.7
Average individual needle weight mg.	29	46	18
Ratio of total needle weight to branch weight	1.4	46.0	17.6
Ratio of one-year needle weight to branch weight	0.9	6.8	5.7

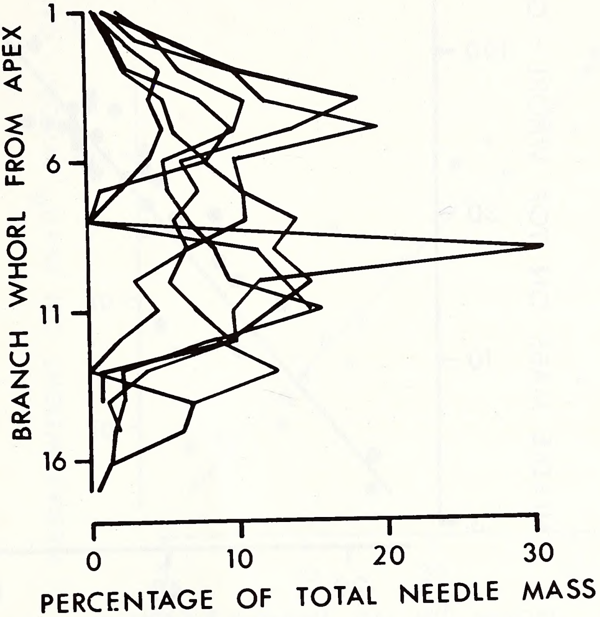

Figure 1. Percentage of total needle weight by branch whorl for seven sample trees.

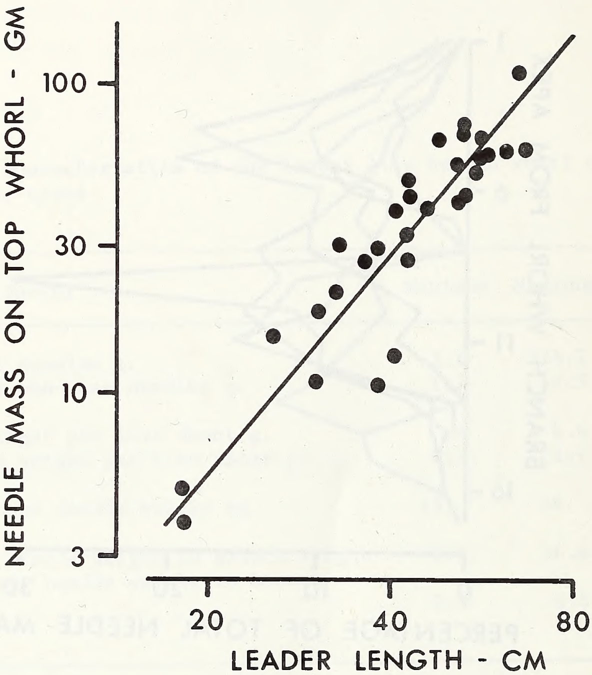

Figure 2. The relationship between leader length and weight of needles on the topmost whorl.

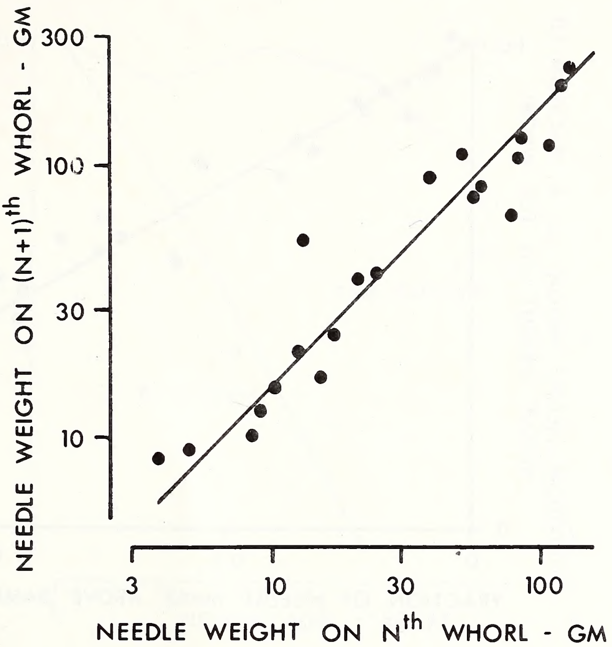

Figure 3. Relative growth in needle mass from whorl to whorl in the upper canopy.

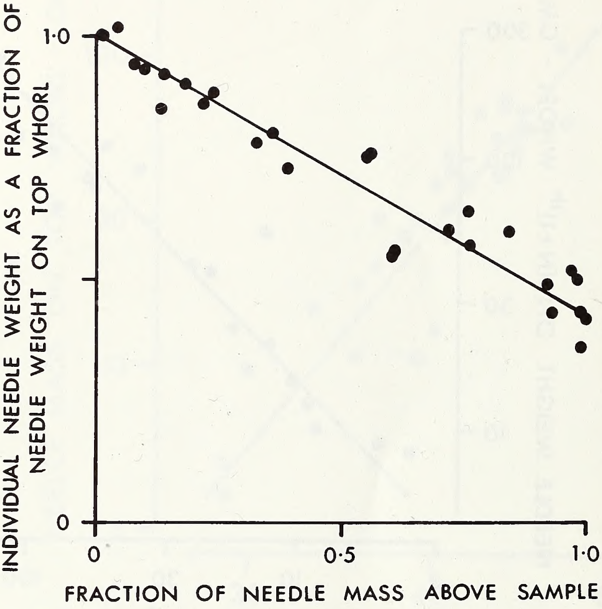

Figure 4. The effect of overlying canopy on the weight of individual needles.

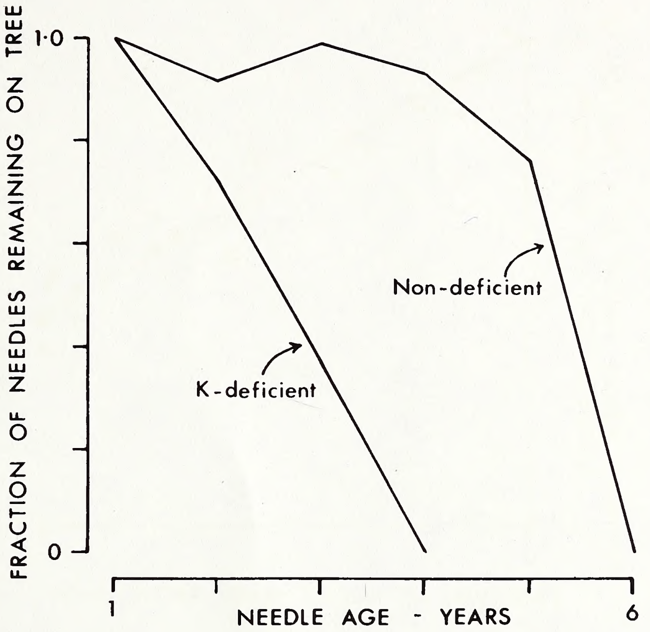

Figure 5. The effect of potassium deficiency on needle longevity.

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